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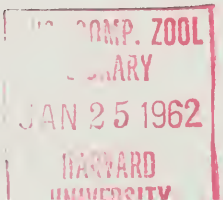

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TULANE STUDIES
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# STUDIES ON THE BACKSWIMMERS OF COSTA RICA
## (HEMIPTERA; NOTONECTIDAE)

JOHN L. DE ABATE,
*DEPARTMENT OF BIOLOGY, UNIVERSITY OF COSTA RICA,*
*SAN JOSE, COSTA RICA*

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NEW ORLEANS

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TULANE STUDIES IN ZOOLOGY

Volume 8, Number 1 April 29, 1960

# STUDIES ON THE BACKSWIMMERS OF COSTA RICA (HEMIPTERA; NOTONECTIDAE)

JOHN L. DE ABATE,
*Department of Biology, University of Costa Rica,*
*San José, Costa Rica*

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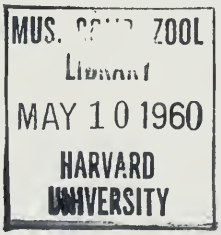


## I. Introduction

Although Costa Rica has a rich fauna, studies of the insects are few. Some early naturalists (Calvert, 1917; Champion, 1897-1901; Picado, 1913; Pittier and Biolley, 1895; Pittier, 1942) published on various species but, with the exception of a recent work (Rosabal, 1954), there has not been any systematic attempt to study related forms at the generic or family levels.

The only records of the Costa Rican Notonectidae are by Champion (1897-1901), Hungerford (1933), and Truxal (1953). After Hungerford's studies on the taxonomic value of male genitalia in aquatic Hemiptera (1919b), Champion's work became obsolete as it was based on external morphology and pigmentation only. Hence, the only reliable information is that of Hungerford and Truxal who reported six forms from occasional collections. In the words of Hungerford: "...surely there are species not yet recognized and more intense collecting and closer scrutiny will prove fruitful indeed..."

In the course of this work, 2,357 specimens were studied, 697 specimens of the genus *Notonceta,* and 1,660 of *Buenoa.* In studying geographic variation in *Buenoa,* many series from various countries were examined. The material was obtained from the Francis Huntington Snow Entomological Collections (FHSC) at the University of Kansas, Museo Nacional de Costa Rica (MNCR), and the author's collection.

*Areas studied.*—Costa Rica, because of its geographic location, is the meeting place of the northern and southern faunas of the hemisphere. Several species common to North and South America have not been repoted in Costa Rica, but their presence is anticipated.

Most of the Costa Rican material studied was obtained from the Central Plateau and adjacent areas.

The Central Plateau is a valley about 1,000 M in altitude, bordered by mountains to the north and south, and by lowlands east and west.

The proximity of both Atlantic and Pacific Oceans provides a relatively homogeneous climate with such a minimum annual oscillation that the climate of the region has been classified as insular (Pittier, 1942). The monthly median temperature for San José, which is a good representation of the region, varies from 18.8°C in January to a median maximum of 20.5°C during May. The extremes range from 16.4°C to 28.1°C. As the annual curve of temperatures reaches just one maximum and one minimum, the climate is considered of tropical type.

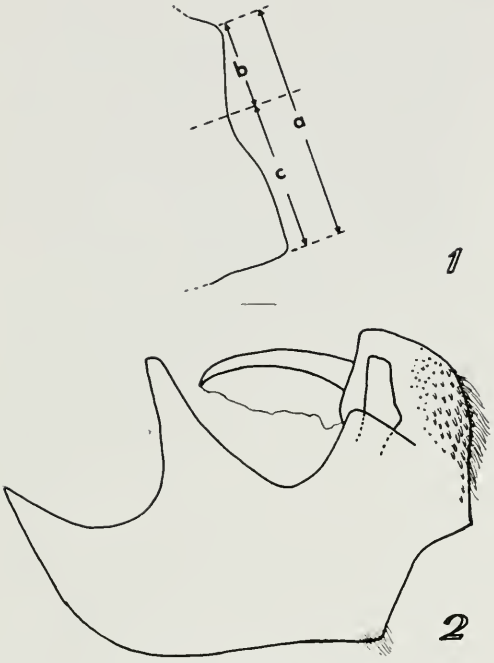
The hydrographic system of the Central Plateau area studied originates in the surrounding mountains, and runs through the plains of the west coast to the Pacific Ocean. The great majority of the rivers (Torres, María Aguilar, Tiribí, Carrizales, etc.) join to form a large stream bearing the name Rio Grande de Tarcoles. The rivers of the Plateau are not large and diminish during the dry season (December to May) but never become dry. During the rainy season (May to November) numerous temporary bodies of water are formed. These are important to the dispersal of the Notonectidae.

The other areas studied in this work (Rio Sucio, Sarapiqui) are in the lowlands north of the Central Plateau, and are irrigated by northward flowing streams that join the San Juan River which empties into the Atlantic Ocean. The high mountains of the Cordillera Volcanica separate this region from the Plateau, leaving a few narrow passages. And finally, the area of San Isidro de El General, in spite of being in the lowlands south of the Plateau, has climatic and hydrographic conditions very similar to the latter.

The vegetation of the Central Plateau is transitional between basal and subalpine. In the east and north, the Plateau is continued as lowland tropical rain forest; to the west it is replaced by grassland prairies which become deserts in the northwest part of the country. To the south the Plateau is continued in part by subtropical forest and grasslands.

*Methods.*—The methods and techniques used in the dissection and clearing of genitalia, study of appendages, measurements and identification, follow those recommended by Hungerford (1933) and Truxal (1953). Illustrations were made with the help of a camera lucida. Pubescence was omitted when it obscured characters of taxonomic importance.

All measurements were made using an ocular micrometer and reticule on a Bausch and Lomb stereoscopic microscope. In measuring the relative position of the curvature in the pronotum for *Notonecta ceres ceres,*




Figures 1-2. *Notonecta ceres ceres*. **1.** Measurements of pronotum: a = total length of side, b = distance from middle of curvature to anterior angle, c = distance from middle of curvature to posterior angle. **2.** Genital capsule, lateral view.

the scheme shown in Figure 1 was used. This computation is expressed in the graphs as a proportion which results from dividing the distance from the middle of the curvature to the anterior angle of the pronotum by the total length of the side of the pronotum.

Graph forms follow the methods of Hubbs and Hubbs (1953) with the exception of the small samples (less than 14) which were computed according to the method described by Cazier and Bacon (1949).

## II. Key to the Males of the Costa Rican Notonectidae [1]

1. Hemelytral commissure without definite hair-lined pit at anterior end. Anterolateral margins of prothorax nonfoveate ..... (*Notonecta*) 2

   Hemelytral commissure with definite hair-lined pit at anterior end. Ventral abdominal keel extending onto last abdominal segment. Males with anterior tarsi two-segmented ..... (*Buenoa*) 5

2. Keel of fourth abdominal sternite bare, the hairs confined to the sides ..... *N. c. ceres*

   Keel of fourth abdominal sternite not bare ..... 3

3. Pronotum broad in front, embracing the eyes, which are flattened and receding from the anterior margin of the vertex. Synthlipsis broad, one half the anterior margin of vertex as seen from above. Scutellum distinctly broader than long. Males with stout tubercle at angle of front trochanter ..... *N. ochrothoe*

   Pronotum not broad in front. Eyes not as above. Males without stout tubercle at angle of front trochanter ..... 4

4. Synthlipsis distinctly less than one half anterior margin of vertex; head prominent ..... *N. indica*

   Synthlipsis wide, one half or more the anterior margin of vertex; head not prominent ..... *N. confusa*

5. Synthlipsis wide, one half or more the anterior margin of vertex ..... 6

   Synthlipsis narrow, less than one half the anterior margin of vertex ..... 10

6. Rostral prong with base originating laterally at or near distal end of third rostral segment ..... 7

   Rostral prong with base not originating laterally at or near distal end of third rostral segment ..... 8

7. Over 7 mm in length. Pronotum with its median length approximately three fifths its humeral width; disc almost unimpressed, not tricarinate ..... *B. crassipes*

   Less than 7 mm in length. Pronotum with its median length approximately two thirds its humeral width; disc with two elongate depressions toward the middle and a large subtriangular depression on each side, thus appearing distinctly tricarinate ..... *B. pallipes*

8. Posterior margin of hind femur with more than forty setae in ventral row ..... *B. pallens*

   Posterior margin of hind fe-

[1] This key was prepared by modification of Hungerford (1933) and Truxal's (1953) keys and includes forms that have not been reported for Costa Rica, but are anticipated because of their distribution north and south of Costa Rica.

mur with less than forty setae in ventral row ..... 9

9. Pronotum almost unimpressed, not tricarinate; length of fore femur two times the width of apex; approximately twenty-five teeth in tibial comb ..... *B. ida*

Pronotum tricarinate; length of fore femur three times or more the width of apex; forty to fifty teeth in tibial comb ..... *B. antigone*

10. Fore femur narrowed at apex; length more than three times the width of apex, the stridulatory area consisting of six to nine sclerotized ridges. Rostral prong equal to or shorter than third rostral segment ..... *B. gracilis*

Fore femur widened at apex; length three times or less the width of apex, the stridulatory area consisting of eleven to fourteen sclerotized ridges. Rostral prong much longer than the third rostral segment ..... *B. platycnemis*

## III. The Notonectidae of Costa Rica

### A. *Notonecta ceres ceres* Kirkaldy, 1897

*Synonymy.*[2] — 1897. *N. mexicana* var. *ceres* Kirkaldy, Trans. Ento. Soc. London, p. 402; 1933. *N. ceres rogersi* Hungerford,

[2] For complete synonymy see: 1933. *N. c. ceres* Kirkaldy; Hungerford, Univ. Kansas Sci. Bull., 34(5) : p. 79.

Figure 3. Localities from which Costa Rican Notonectidae were examined. 1 = Sarapiqui, 2 = Rio Sucio, 3 = Laguna Zarcero, 4 = La Palma, 5 = Laguna San Isidro, 6 = San Jeronimo, Moravia, 7 = Rio Torres, 8 = San José, 9 = Escazu, 10 = Rio Virilla, 11 = Rio Maria Aguilar, 12 = Rio Tiribi, 13 = Desamparados, 14 = Carrizales, Escazu, 15 = San Isidro de El General.

Bull. Univ. Kansas, 34(5): p. 81.

The following description is modified from that of Hungerford (1933) to fit the ranges of variation found in the specimens that I studied.

*Size.*—Length, 10.4 mm to 12.7 mm; width of pronotum, 4.3 to 5.2 mm.

*Color.*—Red and black or tan and black for females; males are typically black but I have found specimens in which red was present in various degrees. Color variations are described in section below on statistical analysis. Anterior half of pronotum, head and limbs yellow or yellowish green; the middle and hind trochanters and femora with the dark stripe of the *N. mexicana* Amyot and Serville group.

*Structural characters.*—Head large; anterior outline of head viewed from above, flattened; vertex a little longer than its anterior width; anterior margin of vertex less convex and plainly shorter than the frontal margin of the eye; anterior breadth of vertex: synthlipsis :: 11 : 3. Pronotum nearly twice the length of head; lateral margins moderately concave and moderately divergent; the margin more concave in females than in males, as seen from the side, strongly curved, pronounced on anterior half; margin of prothorax shorter than the rear margin of the eye below it. Anterior lobe of membrane of hemelytra a little longer than the posterior one. Anterior trochanters of male with moderate hook. Mestotrochanters rounded. The carina of fourth abdominal sternite bare. The terminal abdominal sternite of female narrow, broader at the tip, and broadly incised. First pair of gonapophyses short. Male genital capsule as shown in Figure 2.

*Location of types.*—Kirkaldy collection at U. S. National Museum, Washington.

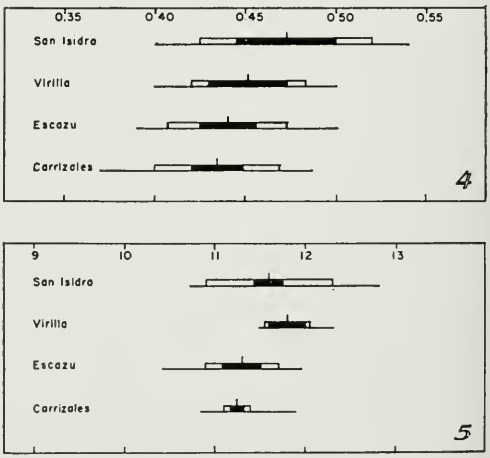
*Comparative notes.*—This subspecies was described by Hungerford (1933) as being different from *N. c. rogersi.* I have found that both are intergrades; a more detailed account is given in the statistical analysis.

*Geographic distribution and specimens studied* (fig. 3).—San José: Aug. 1905, P. Biolley, 1 female, 1 male (FHSC). Rio Virilla: Dec. 1931, H. Schmidt, 9 females, 3 males (FHSC). Rio Tiribi: Aug. 1956, J. De Abate, 2 females, 7 males, 6 nymphs (002);[3] July 1957, J. De Abate, 6 females, 3 males (009); Desamparados: Feb. 1958, S. Jimenez-Canossa, 13 females, 7 males, 42 nymphs (016). San Rafael Escazu: Jan. 1957, S. Jimenez-Canossa, 3 females, 6 nymphs (003). Carrizales, Escazu: Oct. 1957, S. Jimenez-Canossa, 3 females, 1 male, 4 nymphs (012); Nov. 1957, S. Jimenez-Canossa, 5 females, 8 males, 8 nymphs (013); Nov. 1957, S. Jimenez-Canossa, 26 females, 46 males, 205 nymphs (014); Dec. 1957, S. Jimenez-Canossa, 19 females, 26 males, 88 nymphs (015). San Jeronimo, Moravia: July 1956, J. De Abate and L. Mata, 1 females, 3 males (001). La Palma: date unknown, Tristan, 1 male (MNCR); date unknown, P. Biolley, 1 female, 3 males (FHSC). Laguna San Isidro, Heredia: July 1957, J. De Abate and L. Ferrero, 13 females, 13 males, 19 nymphs (008). Rio Sarapiqui: date unknown, H. Schmidt, 2 females, 2 males, 15 nymphs (FHSC). Rio Sucio: date unknown, H. Rogers, 1 female, 1 male (FHSC).

Besides *ceres* this species has another subspecies, *N. c. stirtoni,* which has been reported only for El Salvador.

### 1. *Statistical analysis*

In his monograph on the *Notonecta* of the World, Hungerford (1933) described a new subspecies, *N. c. rogersi.* The characters used in the description were: total




Figures 4-5. *Notonecta ceres ceres.* **4.** Position of the curvature at the side of pronotum. **5.** Total length variation in neighboring populations.

[3] Numbers in parenthesis indicate catalog number in writer's collection.

length, and relative position of the curvature at the sides of the pronotum.

With respect to total length Hungerford established the limit at 12 mm, calling *ceres* the individual which were 12 mm or less in total length and *rogersi* those exceeding that limit. For the other character he wrote: "...The lateral margins of the pronotum of female constricted in front of the middle: *rogersi*...". "...The lateral margins of the pronotum of female constricted near the middle: *ceres*...". However as his arbitrary limit for total length does not correspond to that found in nature, and the description "near the middle" is rather vague, I have analyzed statistically both characters to determine the validity of the subspecific status.

According to Hungerford's descriptions, only seven of the 64 specimens I studied for this purpose could be regarded as *ceres* and seven as *rogersi*. The rest (52 specimens) vary so much that they do not fit completely either description.

Four samples were used in the statistical analysis: 8 specimens from Rio Virilla, 13 specimens from San Isidro de Heredia, 24 from Carrizales de Escazú and 19 from Escazu. In all cases the data refer to adult females, which were selected because they have the curvature more pronounced, and to avoid the introduction of error by using both sexes.

*Position of pronotal curvature.*—The populations analyzed intergrade in such a manner that a subspecific status for this character becomes inconsistent (fig. 4). The samples from Rio Virilla, Escazu, and Carrizales appear to be more closely related to one another than to the one from San Isidro. This perhaps can be correlated with geographic distribution, since the first three areas are about two miles apart, whereas the latter is about ten miles away.

*Total length.*—Although total length is of little taxonomic significance, I attempted to find every possibility for segregation. Figure 5 shows an intergrading situation in which the Rio Virilla sample has higher values than the rest. This variance is not enough to justify a subspecific rank, and it is probably due to ontogenetic variation.

Figure 6 is a scatter-diagram in which the values for the position of the pronotal curvature and total length have been plotted for

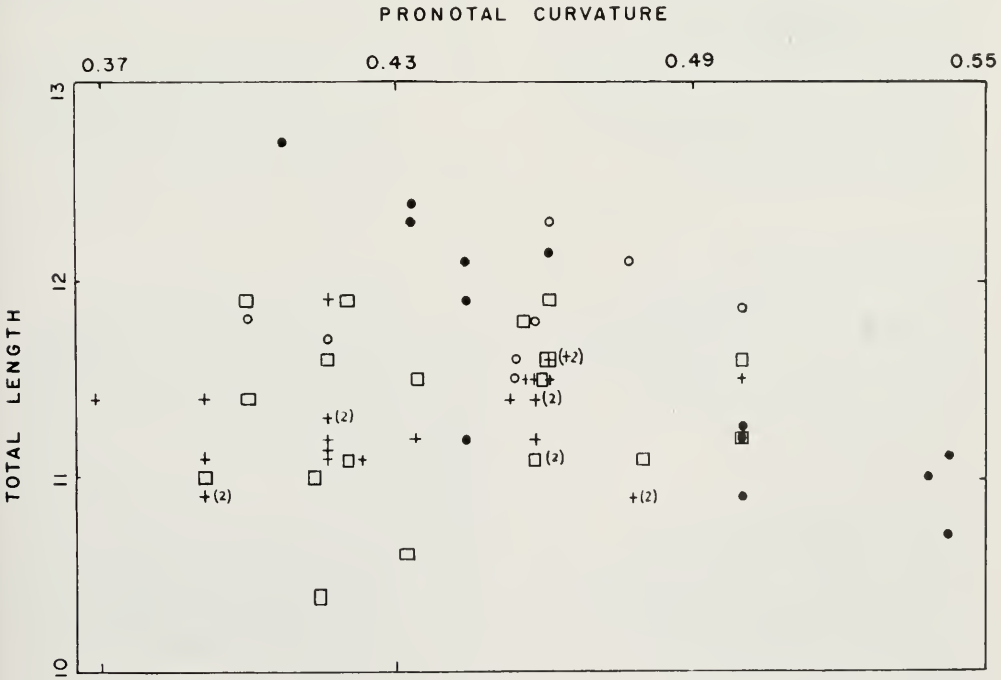



Figure 6. *Notonecta ceres ceres.* Total length compared with relative position of pronotal curvature. Crosses = Carrizales; squares = Escazú; small circles = Rio Virilla; black dots = San Isidro Heredia.

all four samples. Here again we can see that there is not enough segregation of individuals and that *N. c. ceres* has a wide range of variation.

*Conclusions.*—According to this analysis I feel that there is no reason for maintaining the subspecific status for *N. c. rogersi,* which I have relegated to synonymy with *N. c. ceres.*

*Color variation.*—In males there is a gradation in color ranging from the typical black to almost red. This variation concerns only the clavus and corium; the scutellum and membrane are always black.

The 114 specimens studied for this purpose were placed in five representative groups according to coloration (fig. 7). The incidence (by percent) in each group

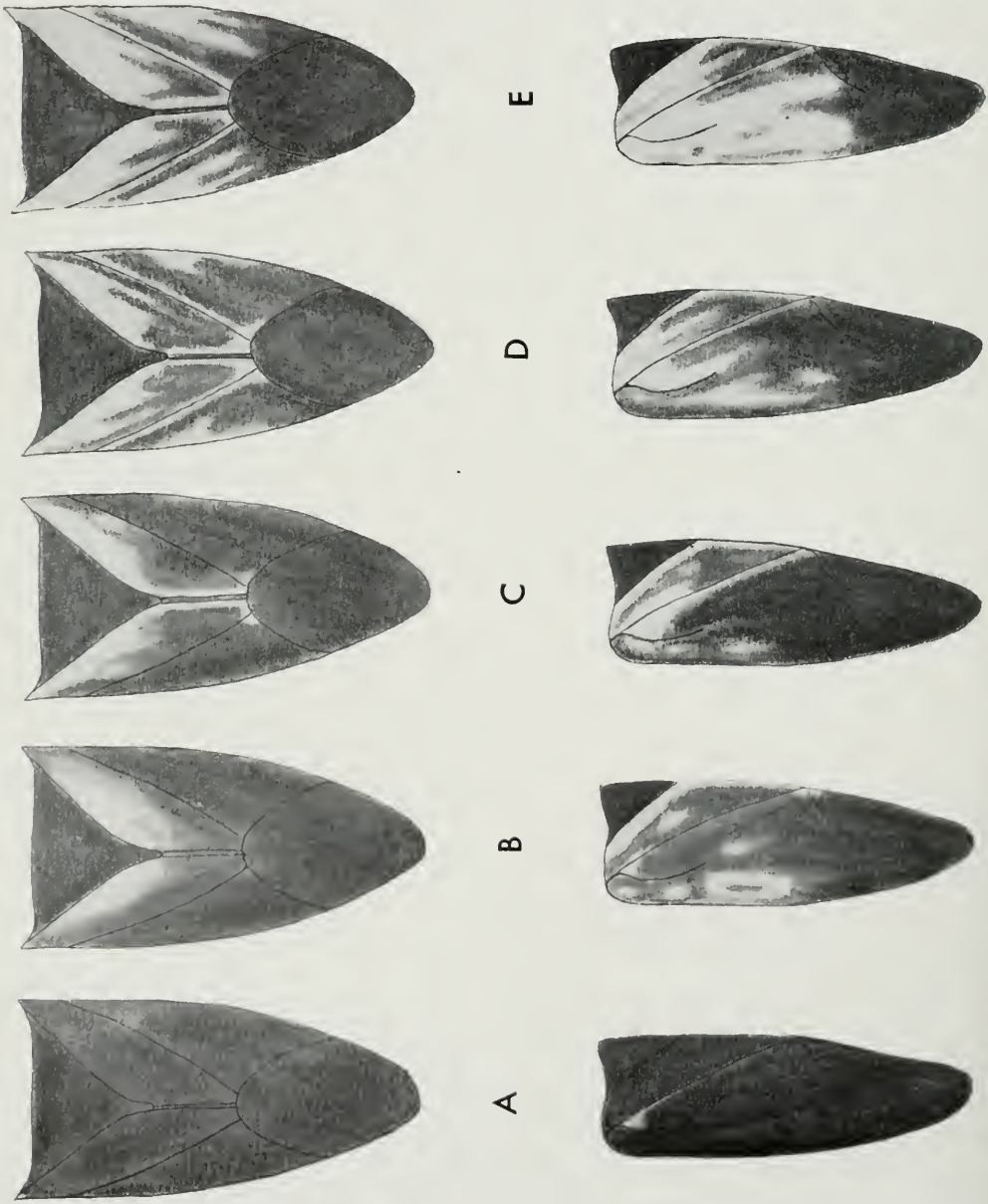



Figure 7. *Notonecta ceres ceres.* Color variation in male hemelytra; upper row, dorsal aspect; lower row, lateral aspect. Red areas shown in white.

is as follows:

| A | B | C | D | E |
|---|---|---|---|---|
| 42.1 | 30.7 | 6.1 | 12.8 | 8.7 |

No significance was found in color variation among different populations. I presume that nutrition and amount of sunlight are the main factors acting on this secondary sexual character. This presumption is based on the observation that male specimens reared in the laboratory are paler and have more red areas than those found in the field.

2. *Life history*

*N. c. ceres* has been reported only for Costa Rica, where it is abundant, but nothing has been published on its life cycle. During the summer of 1957, I had the opportunity to rear a sufficient number of specimens to observe the complete life history of this insect in the laboratory.

The insects used for this purpose were collected from San Isidro de Heredia and Rio Tiribi.

Duration

The life cycle from oviposition to the emergence of the adults requires an average of 65 days. This includes an average incubation period of 20 days at room temperature (23°C±3). The duration of each nymphal instar is from 9 to 11 days at the same temperature.

Eggs

Elongate oval in shape with ventral side flat (fig. 8). Average of 15 eggs measured were: length, 2.2 mm (2.05 to 2.30 mm); width, 0.99 mm (0.90 to 1.05 mm); height, 0.94 mm (0.75 to 1.0 mm). This is one of the largest *Notonecta* eggs known. During the first days the eggs are pearly white, becoming cream colored later. The only external sign of embryonic development is the appearance of two small red spots in dorsal cephalic position, which correspond to the eyes (fig. 8). At hatching the nymphs emerge from a dorsal slit in the egg. In the aquaria, eggs were glued to leaves and stems of *Elodea* sp. and to debris.

Figure 8. Eggs of *Notonecta ceres ceres* attached to stem of *Elodea* sp. Notice how close together the eggs were laid.

Nymphal instars

The nymphal instars are similar, the differences being mostly quantiative. As in the rest of the notonectids, there are five instars.

(I). *First instar* (figs. 9, 14, 19, 24).—Size: length, 3.0 to 3.25 mm; width of body, 1.35 to 1.7 mm; width of head, 1.02 to 1.27 mm; vertex, 0.55 to 0.85 mm; synthlipsis, 0.35 to 0.475 mm. Mean values are given in Table 1.

*Color.*—Limbs and abdomen transparent when newly hatched, becoming white hours later; hairs smoky; eyes red; sides of pronotium and abdomen testaceous; rostrum and antennae testaeceous dark; venter and abdomen light.

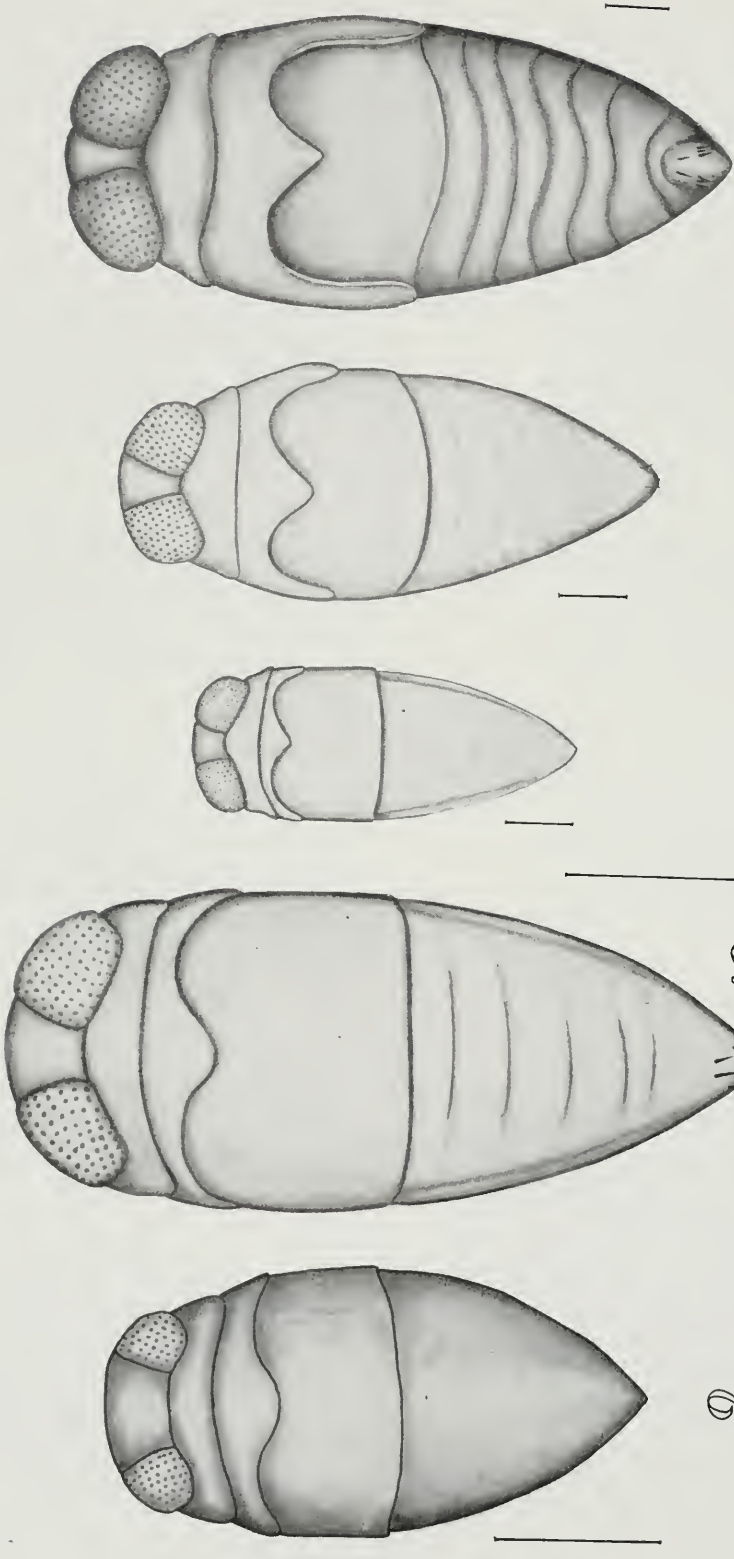
*Structural characters.*—Ventral abdominal carina absent as in all first instars of notonectids. Antennae directed downward, three-segmented, basal segment very short (fig. 19). Anteapical spine of intermediate femora not present (fig. 24). Tarsi one-segmented, ending in two large claws.

(II). *Second instar* (figs. 10, 15, 20, 25).—Size: length, 3.85 to 4.3 mm; body width, 1.35 to 2.25 mm; head width, 1.4 to 1.62 mm; vertex, 0.40 to 0.62 mm; synthlipsis, 0.20 to 0.325 mm. Mean values shown in Table 1.

*Color.*—General facies, white; eyes reddish brown; posterior femora with faint darker zone along the middle, corresponding to the stripe characteristic of the *N. mexicana* group.

*Structural characters.*—Ventral abdominal carina present and marginated with smoky hairs. Antennae three-segmented, oriented as in adults, with a structure as shown in fig. 20. Intermediate femora with anteapical spine moderately developed (fig. 24). Tarsi one-segmented, the posterior with two subequal claws.

(III). *Third instar* (figs. 11, 16, 21, 26).—Size: length, 5.15 to 5.85 mm; width of body, 2.2 to 2.7 mm; width of head, 1.8 to

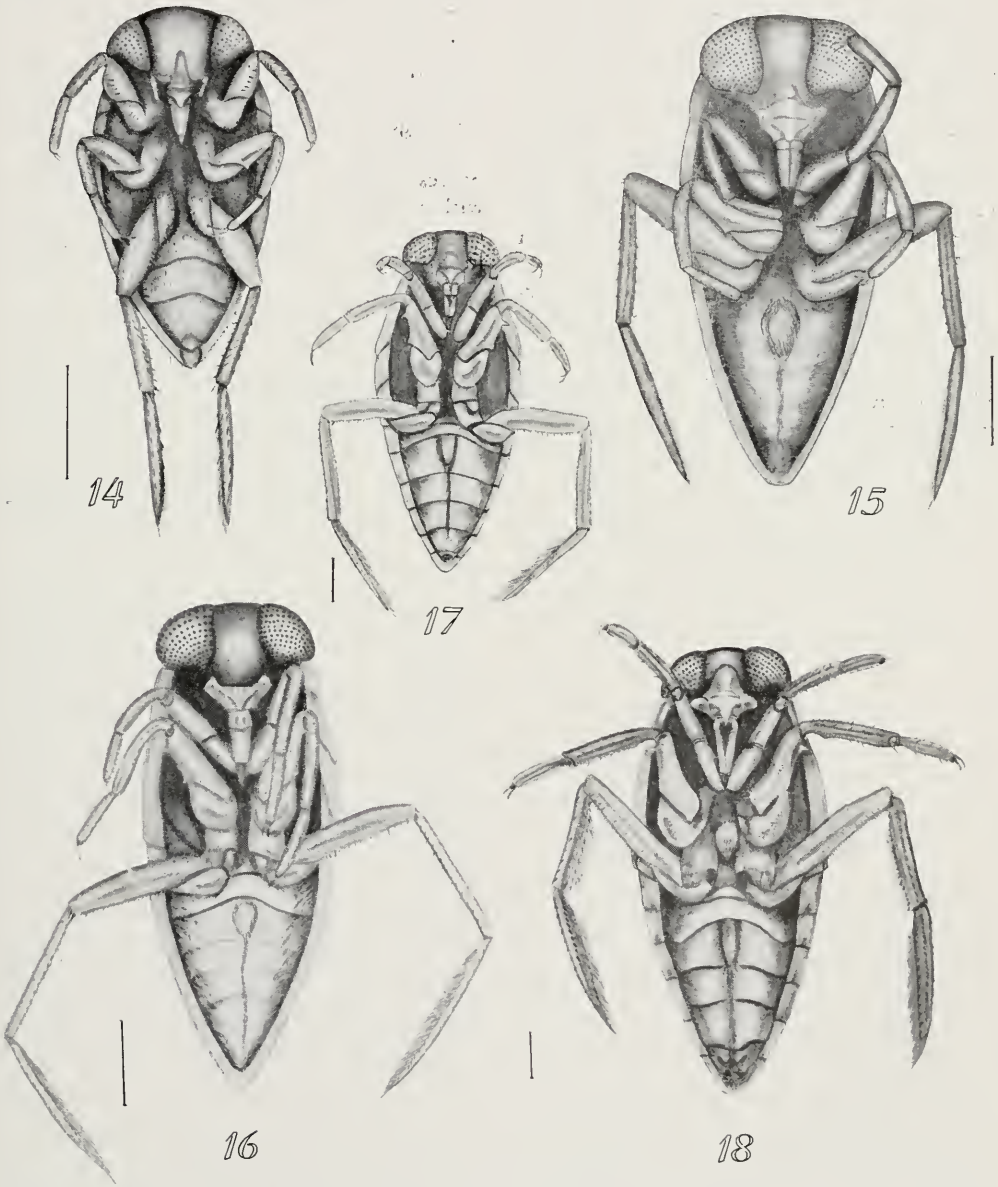



Figures 9-13. *Notonecta ceres ceres.* Dorsal aspect of nymphal instars. **9.** First instar. **10.** Second instar. **11.** Third instar. **12.** Fourth instar. **13.** Fifth instar. Vertical line beside each figure = 1 mm.

2.0 mm; vertex, 0.50 to 0.75 mm; synthlipsis, 0.225 to 0.375 mm. Mean values shown in Table 1.

*Color.*—General facies white; eyes reddish brown, dorsum of abdomen with lateral smoky bands poorly defined. Base of beak and beak dark testaceous. Limbs testaceous, middle trochanters, hind trochanters and femora with the typical markings of the *N. mexicana* group, but not as pronounced as in later instars.

*Structural characters.*—Ventral abdominal carina long, with the hairs darker than in the preceding stage. Antennae located as in adults and with structure as shown in figure 21. Intermediate femora with a hook-like




Figures 14-18. *Notonecta ceres ceres.* Ventral aspects of nymphal instars. **14.** First instar. **15.** Second instar. **16.** Third instar. **17.** Fourth instar. **18.** Fifth instar. Vertical line beside each figure = 1 mm.

TABLE 1.

*N. ceres ceres: extreme ranges and mean values (bold face) for measurements in the nymphal instars.*

| Instar | Specimens Measured | Total Length | Body Length | Head Width | Vertex | Synthlipsis |
|---|---|---|---|---|---|---|
| 1 | 5 | 3.0 -**3.16**-3.25 | 1.35-**1.54**-1.70 | 1.02-**1.19**-1.27 | 0.55-**0.675**-0.85 | 0.35 -**0.405**-0.475 |
| 2 | 15 | 3.85-**4.11**-4.3 | 1.35-**1.84** 2.25 | 1.40-**1.52**-1.62 | 0.40-**0.482**-0.62 | 0.20 -**0.27** -0.325 |
| 3 | 15 | 5.15-**5.49**-5.85 | 2.2 -**2.46**-2.7 | 1.8 -**1.90**-2.0 | 0.50-**0.604**-0.75 | 0.225-**0.308**-0.375 |
| 4 | 15 | 7.25 **7.56**-1.85 | 3.2 -**3.38**-3.5 | 2.25-**2.38**-2.50 | 0.65-**0.756**-0.87 | 0.30 -**0.356**-0.45 |
| 5 | 15 | 9.2 -**9.73**-10.2 | 4.2 -**4.57**-5.1 | 2.9 -**3.0** -3.1 | 0.80-**0.857**-0.95 | 0.30 -**0.36** -0.45 |

anteapical process (fig. 26). Tarsi one-segmented. Wing pads as shown in figure 14.

(IV). *Fourth instar* (figs. 12, 17, 22, 27).—Size: length, 7.25 to 7.85 mm; width of body, 3.2 to 3.5 mm; width of head, 2.25 to 2.50 mm; vertex, 0.65 to 0.87 mm; synthlipsis, 0.30 to 0.45 mm. Mean values shown in Table 1.

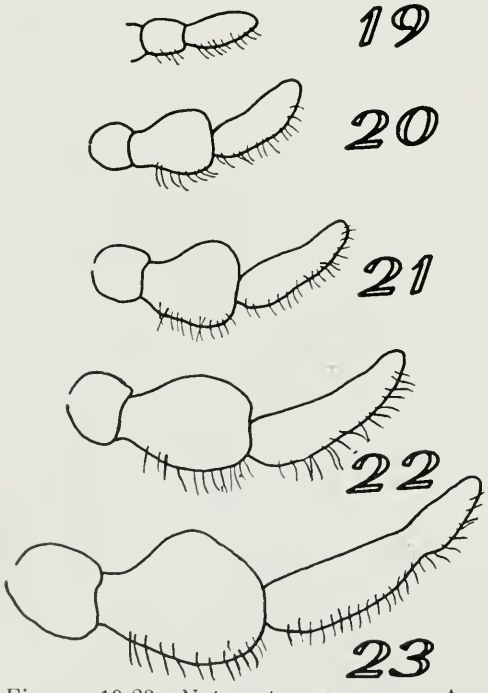
*Color.*—White. Eyes dark brown. Dorsum of abdomen with lateral markings as in third instar. Base of beak and beak testaceous, clypeus darker. Limbs testaceous, all trochanters with median longitudinal stripe; anterior, middle and posterior femora also with the typical stripe of the *N. mexicana* group.

*Structural characters.*—Carina as in third instar. Antennae located as in the preceding stage, with srtucture as shown in figure 22. Intermediate femora with anteapical process straight and well developed, and with a small tubercular process in the middle of the posterior margin (fig. 27). Tarsi as in third instar. Wing pads well developed (fig. 12).

(V). *Fifth instar* (figs. 13, 18, 23, 28). —Size: length, 9.2 to 10.2 mm; width of body, 4.2 to 5.1 mm; width of head, 2.9 to 3.1 mm; vertex, 0.80 to 0.95 mm; synthlipsis, 0.30 to 0.45 mm. Mean values shown in Table 1.

*Color.*—White. Eyes dark brown. Dorsal abdominal markings as in the preceding instar but more distinct. Beak and base of beak as in fourth instar. Ventral aspect darker than in the preceding instars. Limbs as in fourth instar but with darker markings.

*Structural characters.*—Ventral abdominal carina as in the two preceding instars but more pronounced. Eyes strongly confluent posteriorly (fig. 13). Intermediate femora as in fourth instar but with processes more pronounced (fig. 28). Tubercular process in the middle of posterior margin more developed than in the preceding instar. Antennae located as in adults with a constriction in distal third of the third segment. In cleared and mounted antennae, a thin transverse septum can be seen near the level of the constriction (fig. 22) which will become the division between the third and fourth antennal segments of the adult. Wing pads extending beyond posterior thoracic border (fig. 13).




Figures 19-23. *Notonecta ceres ceres.* Antennae of nymphal instars. **19.** First instar. **20.** Second instar. **21.** Third instar. **22.** Fourth instar. **23.** Fifth instar.

## Mating

When collected, many individuals were mating and they continued doing so after transferal to aquaria. This species is able to copulate three times per day, sometimes for periods of three continuous hours (maxi-

TABLE 2.
*N. c. ceres: monthly incidence of the various instars.*

| | | Months | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | J | F | M | A | M | J | J | A | S | O | N | D |
| Instars | 1 | | + | | | | + | | + | + | | + | + |
| | 2 | | + | + | + | | | | + | | + | + | + |
| | 3 | | + | | + | + | + | | + | + | + | + | + |
| | 4 | | + | + | | + | + | + | + | + | + | + | + |
| | 5 | + | + | + | + | + | + | + | + | + | | + | + |
| | Ad. | + | + | + | + | + | + | + | + | + | + | + | + |

mum mating time observed was 3 hrs., 20 min.).

For *N. borealis* Rice (1954) reported that, after mating, there is a preoviposition period. Nothing of this sort was observed in *N. c. ceres,* as females were actively mating during the oviposition period, sometimes laying eggs just a few minutes after copulation.

### Seasonal activity

In all months when collections were made, both adults and nymphs of various instars were found. The stages found and the months involved are given in Table 2. I presume that, due to the favorable climatic conditions of Costa Rica, *N. c. ceres* is able to breed the year around.

### Oviposition

My laboratory notes read as follows "... A gummy substance is secreted on the surface where the eggs is going to be laid. The egg is held by ovopositor against the gummy substance until it is secure. All the process takes about 25 seconds for each egg...".

Eggs are laid in an irregular manner. One isolated female laid 37 eggs in 13 days; that is, an average of 2.8 eggs per day. Four other females laid 76 eggs in 17 dags.

### 3. *Growth*

To obtain estimates of growth rates, nymphs of the five instars were used. The distinct size groups corresponding to each instar are given in Table 1. For every measurement the mean, maximum, and minimum ranges of variation are given. For total length, body width, and head width there is a close isometric relationship. This is not true for the vertex and synthlipsis values where an apparent decrease in growth is detectable at the second instar. This can be explained not as a reduction of vertex and synthlipsis, but as a rapid growth of the eyes in molting to the second instar. The relative size of the eyes can be seen in figures 9, 10, 14, 15. Differential growth between males and females is not given, as sexual determination is difficult during the nymphal instars and the technic involved destroys the specimens.

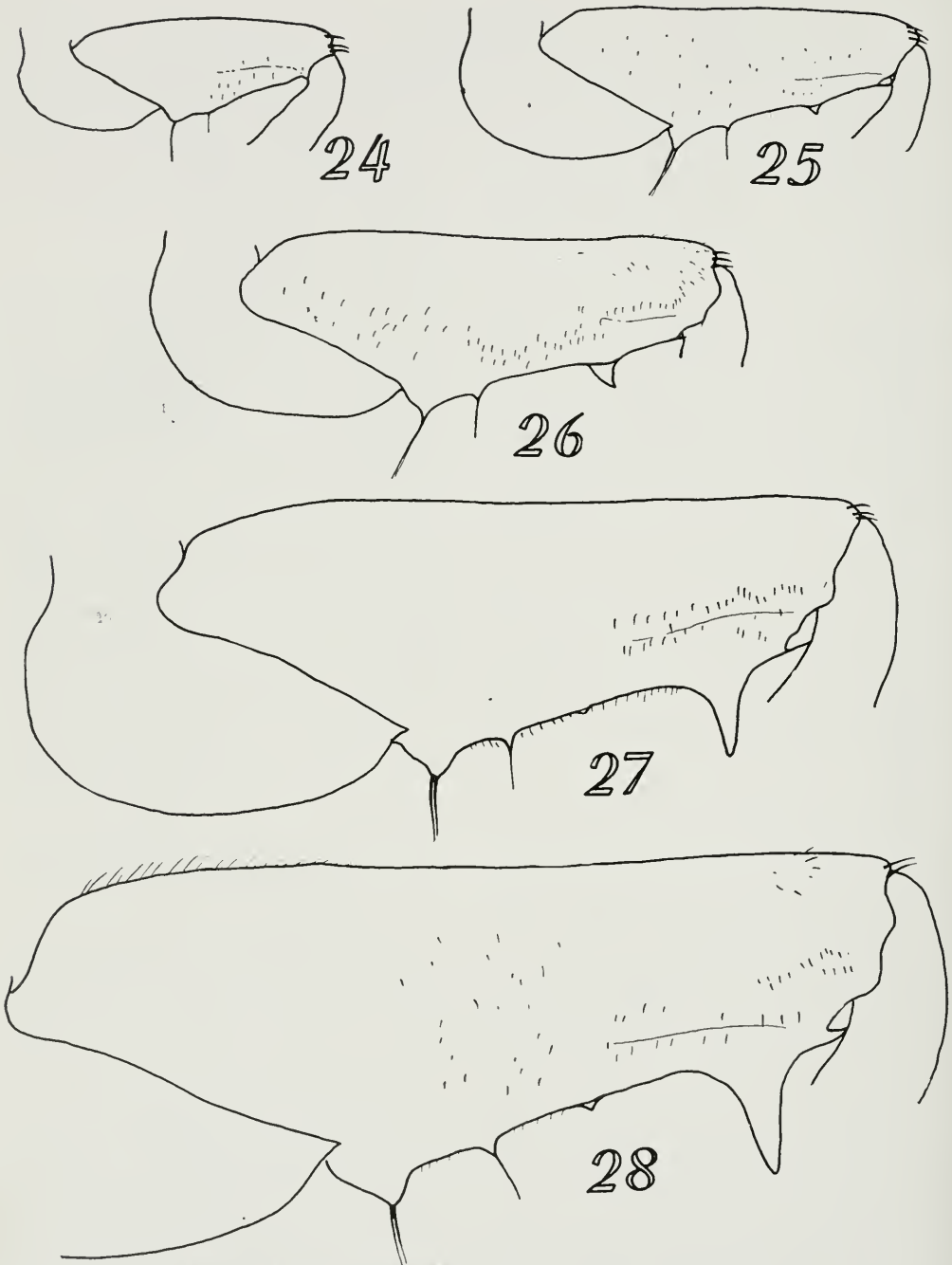
In checking Dyar's Law (1890) in an attempt to establish a definite growth rate for *N. c. ceres,* I found that if a measurement of the first nymphal instar was multiplied successively by 1.3, and again this number by 1.3 a series of figures was obtained that corresponded closely to the values for that particular measurement in the different instars. Table 3 shows these theoretical values compared with the actual averages (taken from Table 1). In all cases the theoretical figures follow closely the actual values.

Knowing the first instar, the measurements of other instars can be foreseen by using the equation:

$$Y = M(1.3)^{N-1}$$

Where Y = the measurement of the nymphal instar sought; M = same measurement in the first instar; 1.3 = the growth factor; and, N = the number of the instar sought in Y.

A further attempt was made to determine the possibility of a unique growth rate, of the measurements studied for all notonectids. For this, data of head width published by Hungerford (1919a) for *N. undulata, N. irrorata* and *Buenoa margaritacea* were used. Also data for *N. insulata, N. borealis, N. raleighi* and *B. limnocastoris* were taken from Rice (1942, 1954). Actual values were compared with the corresponding theoretical figures (Tables 4, 5), and here again the growth rate factor of 1.3 is appropriate. Plotting these figures (figs. 29-32) shows that the theoretical figures follow closely the




Figures 24-28. *Notonecta ceres ceres.* Middle femora of nymphal instars. **24.** First instar. **25.** Second instar. **26.** Third instar. **27.** Fourth instar. **28.** Fifth instar.

actual values for *N. c. ceres, N. insulata, N. undulata, N. irrorata* and *B. margaritacea.* This is not so for the rest of the species studied. For *N. raleighi* the values for third and fifth instars are very close, but not those for the second and fourth. In *N. borealis* and appreciable difference of values can be seen in the fourth instar. And finally,

Table 3.

*N. c. ceres: the actual and theoretical values of growth rate for body parts.*

| Instar | Body Length | | Body Width | | Head Width | |
|---|---|---|---|---|---|---|
| | Actual | 1.3 | Actual | 1.3 | Actual | 1.3 |
| 1 | 3.16 | | 1.54 | | 1.19 | |
| 2 | 4.11 | 4.11 | 1.84 | 2.0 | 1.52 | 1.55 |
| 3 | 5.49 | 5.34 | 2.46 | 2.60 | 1.9 | 2.01 |
| 4 | 7.56 | 6.94 | 3.38 | 3.38 | 2.38 | 2.61 |
| 5 | 9.73 | 9.03 | 4.57 | 4.41 | 3.0 | 3.40 |

Table 4.

*Head width: theoretical and actual growth rate values in five species of Notonecta.*

| Instar | *N. undulata* | | *N. irrorata* | | *N. borealis* | | *N. insulata* | | *N. raleighi* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Actual | 1.3 | Actual | 1.3 | Actual | 1.3 | Actual | 1.3 | Actual | 1.3 |
| 1 | 0.833 | | 0.91 | | 1.045 | | 1.092 | | 0.532 | |
| 2 | 1.06 | 1.083 | 1.2 | 1.18 | 1.375 | 1.358 | ? | 1.419 | 0.95 | 0.691 |
| 3 | 1.4 | 1.41 | 1.56 | 1.54 | 1.815 | 1.766 | 1.85 | 1.845 | 0.97 | 0.899 |
| 4 | 1.87 | 1.833 | 2.08 | 2.0 | 1.935* | 2.295 | 2.3 | 2.399 | 1.3 | 1.169 |
| 5 | 2.5 | 2.382 | 2.86 | 2.6 | 2.805 | 2.984 | 2.86 | 3.118 | 1.5 | 1.519 |

* In Rice (1954) this value is reported as ".935", and is probably an error.

for *B. limnocastoris* a considerable difference is noted in the figures for second and fourth instars.

In the last three cases Rice, who probably obtained the material from field collections and not from laboratory rearing, must have confused some nymphal instars, introducing variations of such magnitude as shown in the curves (figs. 30-32).

Clark and Hersh (1939) studied the growth of *N. undulata:* theirs is a thorough study referring, specially, to growth centers and growth gradients. Applying the 1.3 growth rate factor to their data on head width and body length I found that it corresponded with deviations comparable to those cited in Table 4.

Based on these data, I postulate that the growth rate of body length and head width is very close for all notonectids, if not the same. Further investigation of other species is necessary to establish a generalization in this respect.

*Food.*—*N. c. ceres,* as the rest of the notonectids, has predaceous habits and probably feeds on a great variety of animal forms. In nature I have seen it feeding on *Buenoa* and ostracods. In the laboratory it was fed on muscid flies (*Musca* sp.), tabanid flies (Tabanidae), mosquito larvae (*Culex* sp.), stingless bees (Meliponidae), leaf hoppers (Jassidae) and on small snails (*Tropicorbis* sp.), all of which were accepted eagerly. I also observed that this species attacks and feeds on small fishes (*Rivulus* sp.) and tadpoles (*Hyla* sp.). When specimens were starved, cannibalism was observed.

*Behavior.*—Adults are clumsy swimmers and spend most of the time "hanging" from the surface of the water. When feeding they hold their prey with their front legs, the middle legs hanging with claws just reaching the water surface, and the hind legs with femur and tibia at an angle of about 90° to each other.

When attached to objects under water, they come to the surface to replenish air periodically. Air is stored under the hemelytra and in the ventral abdominal pubescence. The average submergence time, taken from 20 observations, was 4 min., 15 sec., (26 sec. to 4 min., 35 sec.), although Edwards (1953) reported that *Notonecta* are able to remain submerged up to six hours depending on the metabolic rate.

*Ecology.*—In all cases *N. c. ceres* was collected in fresh water. This species was found most commonly in clear, slow-running, permanent, shaded water. In most of the cases, the vegetation was moderate and a sandy-mud bottom was present. For the

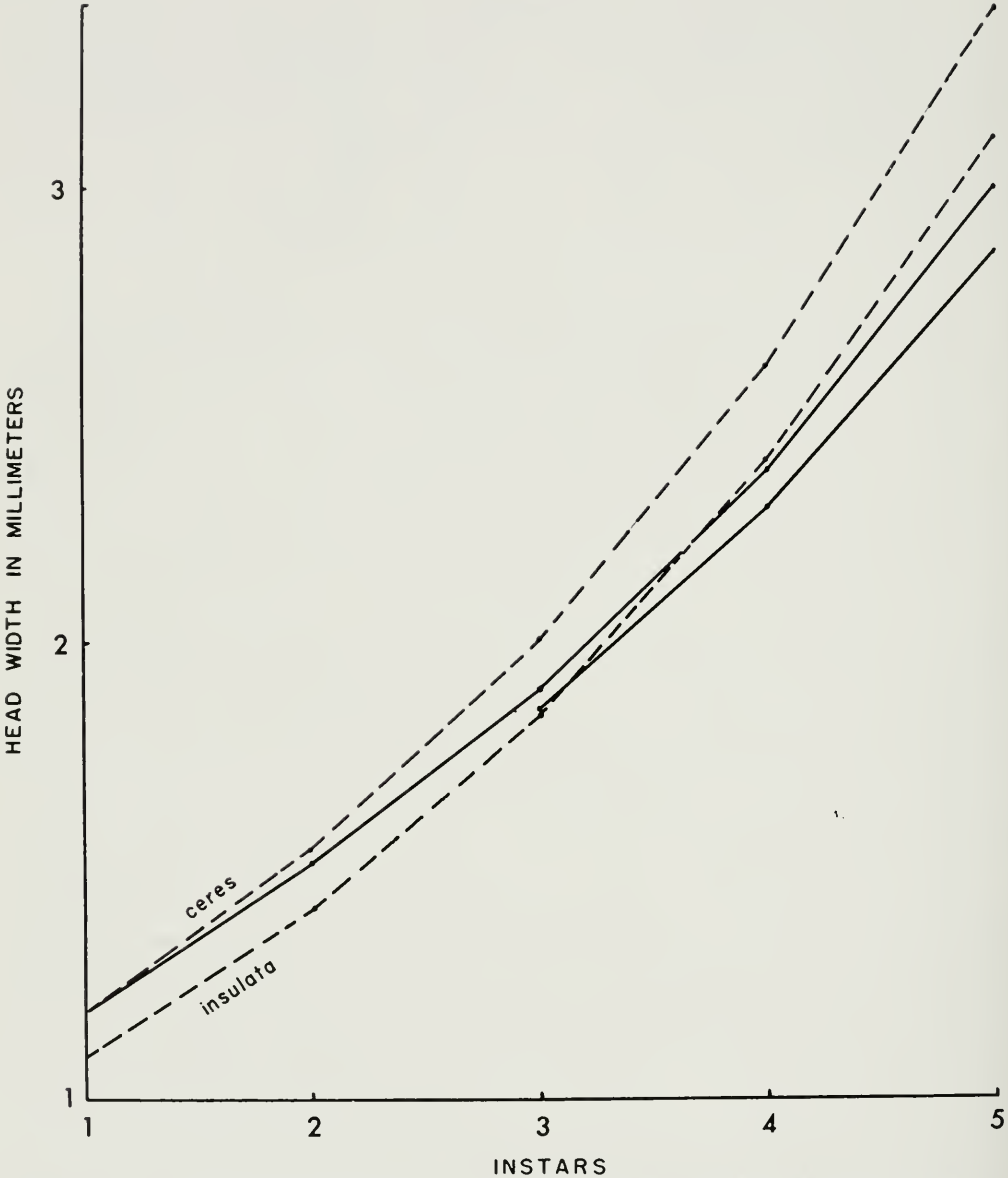



Figure 29. Theoretical and actual growth rates for *Notonecta ceres ceres* and *Notonecta insulata*. Solid lines = actual values; broken lines = theoretical values. Actual data for second instar of *N. insulata* were unavailable.

numerical incidence of each ecological situation see Table 6.

In respect to the fauna, Gerridae, Belostomatidae, ostracods and small fishes and tadpoles were present in various numbers, and I assume that they play an important role in the biology of the notonectids.

*Notonetca indica* Linne, 1771

*Synonymy.*[4]—1771. *N. indica* Linnaeus. Mantissa Plantarum, II, p. 534.

*Size.*—Length, 10 mm to 11 mm, width

[4] For complete synonymy see: 1933. *Notonecta indica* Linne; Hungerford, Univ. Kansas Sci. Bull., 21(9): p. 113.

of pronotum, 3.36 to 3.75 mm.

*Color.*—Luteous to almost black, hemelytra usually white with base of clavus black or tan. Scutellum black, often pale at the tip and basal angles.

*Structural characters.* — Head prominent, more than one half length of pronotum. Anterior margin of vertex straight; width of vertex: synthlipsis :: 5 : 2. Synthlipsis less than one half the anterior margin of the eye. Anterior angles of pronotum embracing the eyes. Anterior trochanter of male with a stout hook. Mesotrochanters rounded or nearly so. Male genital capsule not digitate and with claspers broad; incised at the tip.

*Geographic distribution.* — This species has never before been reported for Costa

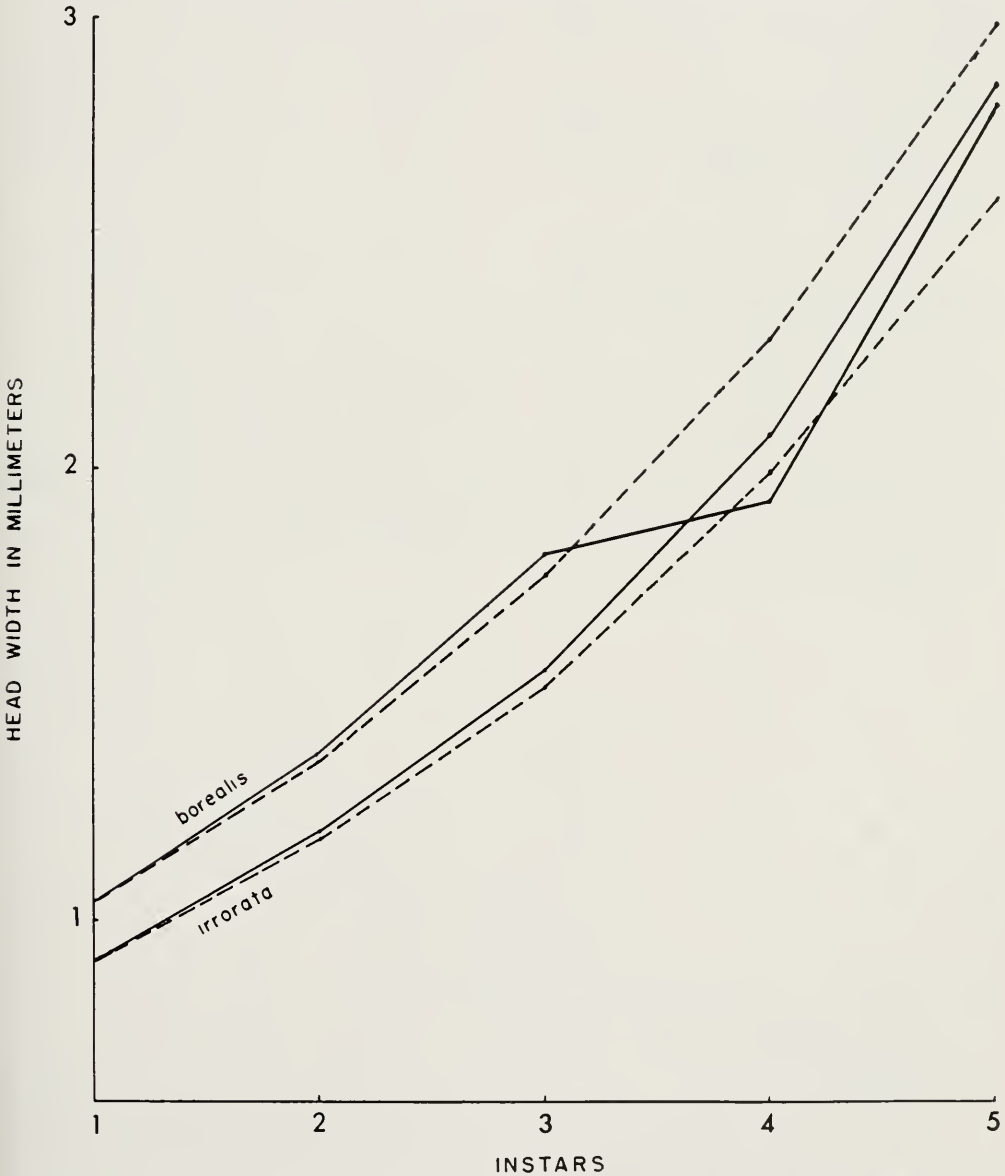



Figure 30. Theoretical and actual growth rates for *Notonecta borealis* and *Notonecta irrorata*. Observe how closely the theoretical values follow the actual values, except for the fourth instar of *N. borealis*. Symbols as in figure 29.

Rica. I collected one male specimen in the San Isidro Heredia Lagoon. In spite of a careful search, I was not able to find another specimen.

Reports on the geographic distribution of this species give a range from 37° latitude in the United States to Brazil in South America. The reports for localities are as follows: United States, Mexico, Guatemala, Colombia, Brazil, and the islands of Cuba, Jamaica, St. Croix, St. Thomas and Puerto Rico. The Costa Rican specimen bears the following data:

Costa Rica: Heredia, Laguna de San Isidro, J. De Abate and L. Ferrero, 1 male (008). This specimen was collected in fresh still water, in a shady area where vegetation was abundant.

C. *Notonecta confusa* Hungerford, 1930

*Synonymy.*—1930. *N. confusa* Hungerford. Bull. Brooklyn Ent. Soc. XXV, p. 140; 1933 *N. confusa* Hungerford; Univ. Kansas Sci. Bull. 34(5): 1-195.

*Size.*—Length, 12 mm; width of thorax, 4 mm.

*Color.*—Pale yellow. Hungerford (1933) stated that the typical color is probably black and white.

*Structural characters.*—This species is very similar to *N. undulata* Say, from which it differs in having the mesotrochanter feebly angulate and the male genital claspers bifurcate. This species was described from a single specimen.

*Geographic distribution.*—The type locality is "South America"; another specimen was reported also from Cuba; I suspect that this species is present in Costa Rica.

D. *Notonecta ochrothoe* Kirkaldy, 1897

*Synonymy.* — 1897. *N. shooterii* var. *ochrothoe* Kirkaldy, Trans. Ent. Soc. London, p. 407; 1905. *N. shooterii* var. *ochrothoe* Kirkaldy; Bueno, J. N. Y. Ent. Soc., xiii, p. 161; 1933. *N. ochrothoe Kirkaldy:* Hungerford, Univ. Kansas Sci. Bull., 34(5), p. 99.

*Size.*—Length, 10.8 to 11.4 mm; width of pronotum, 4.0 to 4.4 mm.

*Color.*—Luteous or pale luteous.

*Structural characters.*—Anterior outline of the head viewed from above, convex; anterior width of vertex: synthlipsis :: 3 : 2. Pronotum more than twice the length of head; anterolateral margins acute and embracing the eyes. Anterior trochanter of male with stout hook and tuberculate projection on the basal angle. Mesotrochanters rounded. Male genital capsule with a thickened protuberance on keel.

*Geographic distribution.* — This species hss not been reported for Costa Rica, but

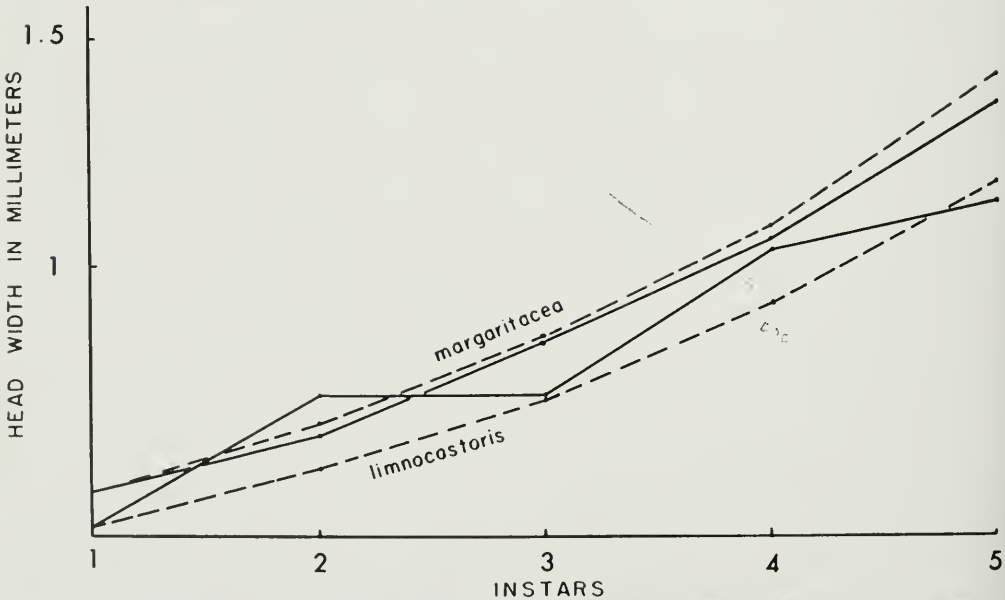



Figure 31. Theoretical and actual growth rates for *Buenoa margaritacea* and *Buenoa limnocastoris*. Compare the closely similar rates in *B. margaritacea* with deviations in *B. limnocastoris*. Symbols as in figure 29.

its presence is anticipated. It has been reported from Colombia, S. A. and California, U. S. A.

E. *Buenoa crassipes* (Champion) Kirkaldy, 1904

*Synonymy.*[5] — 1901. *Anisops crassipes* Champion. Biologia Centrali - Americana, Heteroptera, vol. II, p. 374.

*Size.*—Male, length 7.0 to 8.4 mm; head width, 1.75 to 2.2 mm; vertex 0.26 to 0.35 mm; synthlipsis, 0.10 to 0.21 mm. For the female Truxal (1953) reports the following figures: length, 5.98 to 7.5 mm; greatest body width, 1.75 to 2.01 mm.

*Color.*—General facies testaceous to nigro-violaceous. Head, pronotum, venter and limbs testaceous. Keel and portions of conexivum testaceous. This species is variable in color.

*Male structural characters.*—Viewed from above, head is laterally rounded with vertex indented. Greatest width of head from six to seven times the width of vertex. Synthlipsis approximately half the width of vertex. Tylus slightly inflated. Rostral prong with apex rounded, its origin near the distal end of third rostral segment. Fore femur with triangular and subtriangular stridulatory area formed by ten to eighteen ridges. Genital claspers normal.

*Female structural characters.*—Head shaped as in males, five and one half times the width of vertex. Synthlipsis approximately one half the width of vertex. Scutellum with median length greater than that of pronotum. Ovipositor normal in shape, with teeth arranged in two longitudinal rows. The inner row with large teeth, the outer row with smaller teeth.

TABLE 5.

*Head width: theoretical and actual growth rate values in two species of Buenoa.*

| Instar | *B. limnocastoris* Actual | 1.3 | *B. margaritacea* Actual | 1.3 |
|---|---|---|---|---|
| 1 | 0.45 | | 0.5 | |
| 2 | 0.715 | 0.546 | 0.625 | 0.65 |
| 3 | 0.715 | 0.709 | 0.832 | 0.845 |
| 4 | 1.04 | 0.923 | 1.063 | 1.098 |
| 5 | 1.15 | 1.199 | 1.365 | 1.428 |

*Geographic distribution.* — This species has been reported for Guatemala, Costa Rica, Ecuador and Brazil. Specimens from the following localities were studied:

Costa Rica: Heredia, Laguna Zarcero La Peña: Jan. 1957, J. Vieto, 6 females, 14 males, 5 nymphs (004); Laguna San Isidro, Aug. 1957, J. De Abate, 2 females, 10 males, 27 nymphs (008). San José; purchased June 1931, H. Schmidt, 20 females, 6 males (FHSC); June and July 1931, H. Schmidt, 11 females, 10 males (FHSC); purchased 1932, H. Schmidt, 82 females, 58 males (FHSC); Rio Virilla, Dec. 1931, H. Schmidt, 33 females, 21 males (FHSC); Rio Torres, Feb. 1932, H. Schmidt, 1 female, 1 male, 1 nymph (FHSC); Heredia, Rio Sarapiqui, H. Schmidt, 8 females, 8 males (FHSC).

Brazil: Sta. Catarina, Nova Teutonia, Dec. 1946, F. Plaumann, 20 females, 34 males (FHSC); Nova Teutonia, May 1948, F. Plaumann, 42 females, 23 males (FHSC).

*Ecology.*—*B. crassipes* was found in fresh, clear, static, permanent, exposed waters. The incidence of this species in waters completely exposed to the sun perhaps can be explained studying their behavior. These notonectids spend most of their time swimming gracefully or resting about four inches below the water surface, thus posibly having protection from the sun.

F. *Buenoa pallens* (Champion) Kirkaldy, 1904

*Synonymy.*[6] — 1901. *Anisops pallens* Champion. Biologia Centrali - Americana, Heteroptera, Vol. II, p. 374.

*Size.*—Male: total length, 5.6 to 7.3 mm; head width, 1.4 to 1.9 mm; vertex, 0.23 to 0.37 mm. Truxal (1953) reports the following figures for the female: length, 5.98 to 7.15 mm; greatest body width, 1.75 to 2.01 mm.

*Color.*—Pale testaceous to nigro-violaceous. Light specimens with ventral keel and last two segments testaceous. Dark specimens with head, anterior pronotum, venter and limbs testaceous. Scutellum usually black with apex testaceous or sordid white. This species is variable in color.

*Male structural characters.*—Viewed from

[5] For complete synonymy see: 1953. *Buenoa crassipes* (Champion); Truxal, Univ. Kansas Sci. Bull., 35(11): p. 1385.

[6] For complete synonymy see: 1953: *Buenoa pallens* (Champion); Truxal. Univ. Kansas Sci. Bull., 35(11); p. 1414.

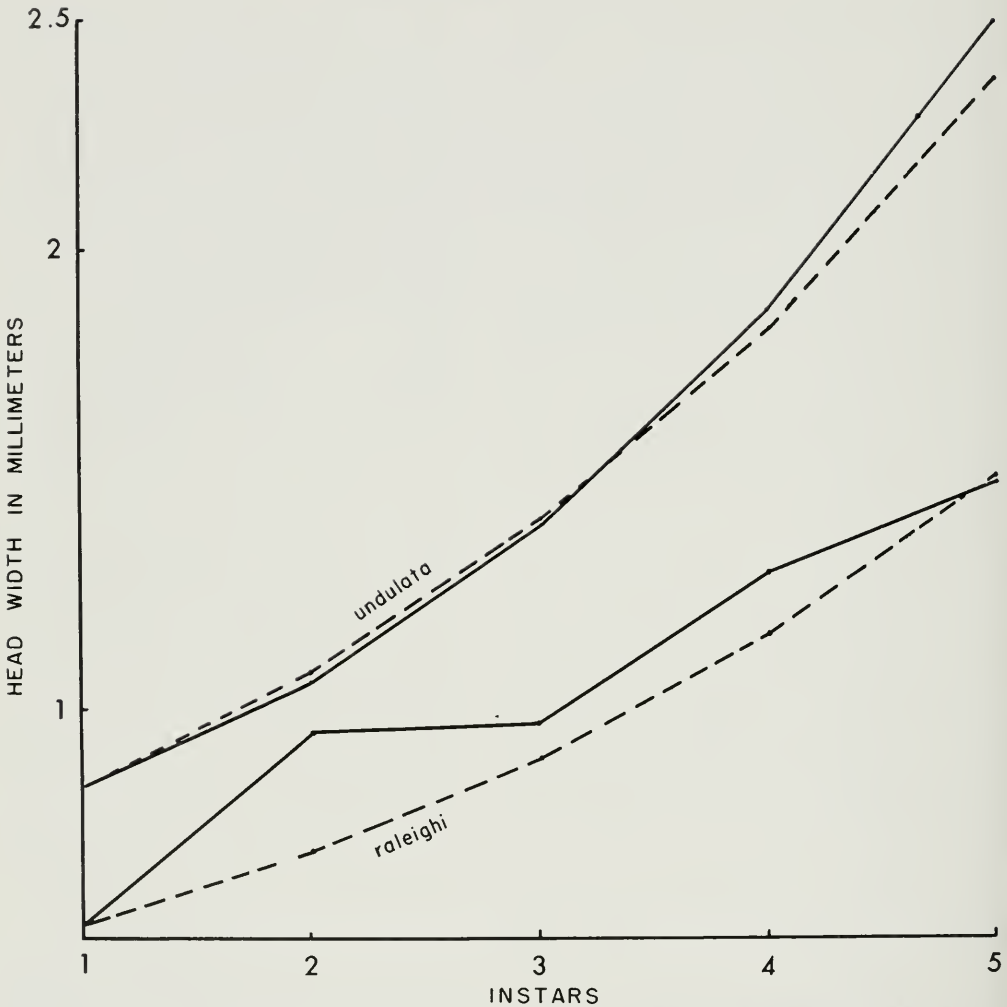



Figure 32. Theoretical and actual growth rates for *Notonecta undulata* and *Notonecta raleighi*. Observe closely similar actual and theoretical rates for *N. undulata;* note the discrepencies in second and fourth instars of *N. raleighi*. Symbols as in figure 29.

above, head laterally rounded with vertex indented. Greatest width of head less than seven times the width of vertex. Synthlipsis narrow, about three fifths the anterior width of vertex. Tylus slightly inflated; rostral prong variable in shape, its origin not at the distal end of the third rostral segment. Fore femur with triangular or subtriangular stridulatory area formed by sixteen to twenty-two ridges. Genital claspers normal.

*Female structural characters.*—Head shaped as in males, its width approximately five and one-half times the width of vertex. Synthlipsis approximately one-half the width of vertex. Scutellum large, with median length greater than the length of pronotum. Ovipositor normal in shape, with the teeth arranged in two rows. The inner row of few large teeth; the outer row of smaller teeth.

*Geographic distribution.—B. pallens* has been recorded for Mexico, Guatemala, Costa Rica, St. Thomas, St. Croix, Guadeloupe, Dominica, Grenada, Trinidad, Colombia, Ecuador, Brazil, Peru and Chile. Specimens from the following localities were studied:

Mexico: Morelos, Cuernavaca, Oct. 1936, H. D. Thomas, 126 females, 40 males (FHSC). Oaxaca, Aug. 1937, H. D. Thomas,

30 females, 11 males (FHSC).

Costa Rica: San José, Maria Aguilar, Oct. 1957, S. Jimenez-Canossa, 7 females, 8 males, 1 nymph (011); Carrizales, Escazu, Oct. 1957, S. Jimenez-Canossa, 31 females, 26 males, 22 nymphs (012); Carrizales, Escazu, Oct. 1957, S. Jimenez-Canossa, 6 females, 3 males, 4 nymphs (0.14); Carrizales, Escazu, Dec. 1957, S. Jimenez-Canossa, 4 females (015).

St. Croix: Christiansted, June 1941, H. A. Beatty, 1 female, 3 males (FHSC).

Peru: Cajamarca, Celendin, May and June 1936, F. Woytkowsky, 127 females, 117 males (FHSC); Amazonas, Chachapoyas, Aug. 1936, F. Woytkowsky, 36 females, 44 males (FHSC).

*Ecology.*—Specimens of this species were found more commonly in fresh, clear, static, permanent, shaded waters. For the numerical incidence of each ecological character see Table 4

### G. *Buenoa pallipes* (Fabricius) Kirkaldy, 1904

*Synonymy.*[7] — 1803. *Notonecta pallipes* Fabricius. Systema Rhyngotorum, p. 103.

*Size.*—Male: total length, 5.3 to 6.8 mm; head width, 1.4 to 1.7 mm; vertex, 0.20 to 0.30 mm; synthlipsis, 0.09 to 0.15 mm. For the female Truxal (1953) gives the following figures: length, 5.62 to 6.50 mm; greatest body width, 1.69 to 1.95 mm.

*Color.*—Sordid white to black. Pronotum usually fuscous; scutellum black or fuscous, with apex testaceous. Abdomen black except for ventral keel and portions of conexivum. This species is variable in color, a wide color gradation being found within a single population.

*Male structural characters.*—Viewed from above, outline of head laterally rounded, its width six times the width of vertex. Synthlipsis narrow, approximately one-half the width of vertex. Tylus inflated; rostal prong with posterior margin almost straight, its base originating at distal end of third rostral segment. Fore femur with a subtriangular stridulatory area consisting of approximately seventeen ridges. Male genital claspers normal.

*Female structural characters.*—Head shaped as in males, its width about six times the width of vertex. Synthlipsis as in males. Scutellum large, its median length greater than that of pronotum. Ovipositor normal in shape, with teeth arranged in two lateral rows. The inner row with large teeth, the outer row with smaller teeth.

*Geographic distribution.*—*B. pallipes* has been reported for Hawaii, Mexico, Honduras, Costa Rica, Panama, Jamaica, Puerto Rico, St. Thomas, Guadeloupe, St. Vincent, Colombia, Peru and Paraguay. I had the opportunity of studying specimens from the following localities:

Honduras: Tela, Apr. 1923, J. Deal, 93 females, 76 males (FHSC).

Jamaica: Montego Bay, Lumsden Tydenham, St. Ann, Feb. 1928, L. G. Perkins, 7 females, 3 males (FHSC); Baron Hill Trelawny, Feb. 1928, L. G. Perkins, 1 female, 1 male (FHSC); Bath St. Thomas, Mar. 1937, Ch. Roys, 19 females, 8 males (FHSC).

Costa Rica: Cartago, San Isidro de El General, Feb. 1939, D. L. Rounds, 1 female, 1 male (FHSC).

Peru: Amazonas, Guayabamba, Aug. 1936, F. Woytkowsky, 70 females, 67 males (FHSC).

Paraguay: Villarrica, Dec. 1924, F. Schade, 28 males (FHSC).

*Ecology.*—No data on the ecology of this species is available. I have not been able to collect it although it was recorded from Costa Rica by Truxal (1953).

### H. *Buenoa platycnemis* (Fieber) Truxal, 1953

*Synonymy.*[8]—1851. *Anisops platycnemis* Fieber. Abhandlungen Kongl. Bohmishen Gesellschaft Wissenschaften, Vol. VII, Series 5, p. 485.

*Size.*—Male: total length, 4.4 to 5.8 mm; head width, 1.1 to 1.4 mm; vertex, 0.19 to 0.28 mm; synthlipsis, 0.06 to 0.14 mm. Truxal (1953) reported the following measurements for the female: length, 5.00 to 5.43 mm; greatest body width, 1.49 to 1.75 mm.

*Color.*—Sordid white to black. Head, parts of pronotum, thoracic venter and limbs sordid white to testaceous. Scutellum usually

[7] For complete synonymy see: 1953. *Buenoa pallipes* (Fabricius); Truxal, Univ. Kansas Sci. Bull., 35(11): p. 1418.

[8] For complete synonymy see: 1953. *Buenoa platycnemis* (Fieber); Truxal, Univ. Kansas Sci. Bull., 35 (11): p. 1421.

testaceous or black with apex lighter. Abdominal venter black with keel and parts of conexivum testaceous.

*Male structural characters.*—Viewed from above, head laterally rounded. Greatest width of head five to six times the width of vertex. Synthlipsis narrow, less than one-half the width of vertex. Tylus moderately inflated; rostral prong longer than third rostral segment and originating at distal end of the third rostral segment. Fore femur with subtriangular stridulatory area formed by eleven to fourteen ridges. Genital claspers normal.

*Female structural characters.*—Head shaped as in males, its width five to five and one half times the width of vertex. Synthlipsis less than half the width of vertex. Scutellum large with median length greater than that of pronotum. Ovipositor of normal shape with teeth arranged in two rows; the inner row of large teeth, the outer row of small ones.

*Geographic distribution.* — This species has been reported for the United States (Texas and Florida), Mexico, Cuba, Grand Cayman, Haiti, Jamaica, Mona, Puerto Rico, St. Thomas, St. Croix, Martinique, Costa Rica, Panama, Colombia, Venezuela, Brazil and Peru. Specimens from the following localities were studied:

Mexico: Sonora, Rio Mayo, Feb. 1935, H. E. Gentry, 19 females, 8 males (FHSC). Michoacan, El Sabino Uruapan, July 1936, H. D. Thomas, 19 females, 19 males (FHSC). Campeche, Hda. Encarnacion, Oct. 1936, H. D. Thomas, 5 females, 6 Males (FHSC).

U. S. A.: Texas, Mc Allen, Nov. 1932, L. D. Tuthill, 4 females, 6 males, (FHSC); Star Co., July 1938, R. I. Sailer, 5 females, 7 males (FHSC); Falfurrias, Jan. 1946, L. D. Beamer, 2 females, 2 males (FHSC).

Florida: L. Matecumba Key, Mar. 1947, R. H. Beamer and L. D. Beamer, 6 females, 5 males (FHSC).

Grand Cayman: Cow well near Pedro Castle, Oxford Univ. Biol. Exp., Aug. 1928, Lewis and Thompson, 11 females, 11 males (FHSC).

Cuba: Habana Bot. Garden, Jan. 1932, P. J. Bermudez, 8 females, 6 males (FHSC); Habana, 1933, P. J. Bermudez, 14 females, 31 males (FHSC).

Puerto Rico: Luquillo July 1932, J. Blanch, 1 female, 2 males (FHSC); Quebrada, Feb. 1935, J. G. Diaz, 2 females, 1 male (FHSC); Florida Road, Feb. 1935, J. G. Diaz, 10 females, 5 males (FHSC);

TABLE 6.
*Ecological data.*

| | | *N. c. ceres* | *Buenoa crassipes* | *Buenoa pallens* | *N. indica* |
|---|---|---|---|---|---|
| | Number of collection sites | 15 | 2 | 5 | 1 |
| Vegetation | Abundant | 20% | 100% | 20% | |
| | Moderate | 80% | | 80% | 100% |
| Bottom | Sand | 13.3% | 50% | | |
| | Mud | 20 % | | 20% | |
| | Sandy mud | 66.6% | 50% | 80% | 100% |
| Water | Dark | 20% | | 20% | |
| | Clear | 80% | 100% | 80% | 100% |
| | Flowing | 53.3% | | 40% | |
| | Static | 46.7% | 100% | 60% | 100% |
| | Temporary | 26.7% | | 40% | |
| | Permanent | 73.3% | 100% | 60% | 100% |
| | Shaded | 73.3% | | 60% | |
| | Exposed | 26.6% | 100% | 40% | 100% |

Almirante Road, March 1935, J. G. Diaz, 8 females, 5 males (FHSC); Tortuguera L., Mar. 1935, J. G. Diaz, 8 females, 3 males (FHSC); Near Isabela, May 1935, J. G. Diaz, 2 females, 7 males (FHSC); Luquillo Mts., Nov. 1935, J. G. Diaz, 8 females, 4 males (FHSC).

Costa Rica: Cartago, San Isidro de El General, Feb. 1939, D. L. Rounds, 1 female, 4 males (FHSC).

Colombia: Villavieja, 1944, R. A. Stirton, 26 females, 22 males (FHSC).

Peru: Amazonas, Vic. Guyabamba, Aug. 1936, F. Woytkowsky, 23 females, 28 males (FHSC); San Martin, Vic. Rioja, Sept. and Oct. 1936, F. Woytkowsky, 11 females, 11 males (FHSC).

*Ecology.*—There are no reports on the ecology of this species. Only five specimens have been collected in Costa Rica and they bear no ecological data. I have not been able to collect this species.

I. *Buenoa antigone antigone* (Kirkaldy) Truxal, 1953

*Synonymy.*[9] — 1899. *Anisops antigone* Kirkaldy, G. W. The Entomologist, vol. XXXII, p. 30.

*Size.*—Male: length, 7.80 to 7.99 mm; greatest body width, 2.46 to 2.60 mm; female: length, 8.25 to 8.51 mm; greatest body width, 2.60 to 2.79 mm.

*Color.* — Testaceous; scutellum usually ochraceous, brown at the base. Ventral abdomen brown or black with conexivum testaceous.

*Male structural characters.*—Head laterally rounded when viewed from above, its width more than six times the width of vertex. Synthlipsis one half to two thirds the width of vertex. Rostral prong originating laterally at proximal end of third rostral segment. Fore femur with triangular stridulatory area consisting of fifteen to twenty-three ridges. Genital claspers normal.

*Females structural characters.*—Head as in males. Synthlipsis more than half the width of vertex. Ovipositor with two rows of teeth all small except for the apical four in the outer row.

*Geographic distribution.*—Recorded from Mexico, Guatemala, Cuba, Grand Cayman, Haiti, Jamaica, Puerto Rico, St. Croix, Brazil, Ecuador, Peru, Bolivia, Paraguay and Argentina. Because of the recorded geographic distribution, the presence of this species in Costa Rica is expected.

J. *Buenoa gracilis* Truxal, 1953

*Synonymy.*—1953. *Buenoa gracilis* Truxal, Univ. Kansas Sci. Bull. XXXV(11), p. 1439.

*Size.*—Male: length, 5.39 to 6.04 mm; greatest body width, 1.30 to 1.49 mm; female: length, 5.52 to 6.11 mm; greatest body width, 1.36 to 1.69 mm.

*Color.*—Sordid white. Abdominal venter black except keel and portions of conexivum, sordid white to pale testaceous.

*Male structural characters.*—Viewed from above, outline of head laterally rounded; greatest width of head, six to six and one half times the width of vertex. Synthlipsis narrow, approximately one-fourth the width of vertex. Tylus inflated; rostral prong originating near the proximal end of third rostral segment. Fore femur with subtriangular stridulatory area consisting of about six to nine ridges. Male genital claspers normal.

*Female structural characters.*—Head shaped as in males, its width approximately five times the width of vertex. Pronotum faintly tricarinate; scutellum with median length greater than that of pronotum. Ovipositor normal in shape, with two rows of teeth; the inner row of large teeth and the outet row of smaller teeth.

*Geographic distribution.*—Reported from Mexico, Honduras, Panama, Cuba, Jamaica, Puerto Rico, St. Croix, Grenada, and Peru. This species is probably present also in Costa Rica.

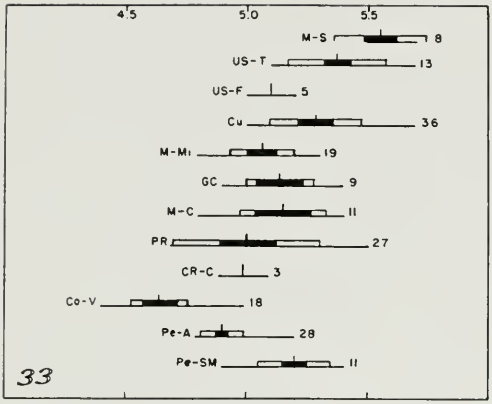
K. *Buenoa ida* Kirkaldy

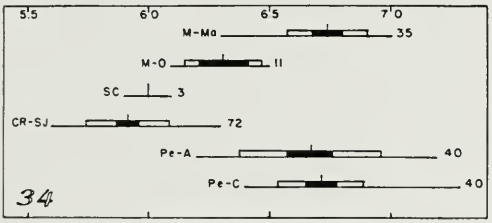
*Synonymy.*—1904. *Buenoa ida* Kirkaldy, G. W., Wiener Ziet., Vol. XXIII, pp. 121, 122 and 134; 1909. *Buenoa ida* Kirkaldy, G. W. and Torre-Bueno, J. R. de la. Proc. Ent. Soc. Washington, vol. X, p. 200. (catalogue); 1953. *Buenoa ida* Kirkaldy; Truxal. Univ. Kansas Sci. Bull., 35(11), p. 1383.

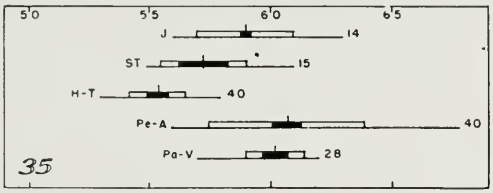
*Size.*—Male: length, 9.16 to 9.62 mm; greatest body width, 2.73 to 2.82 mm; female: length, 9.29 to 9.94 mm, greatest body width, 3.12 to 3.25 mm.

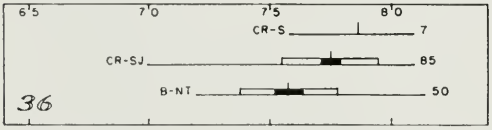
*Color.*—Fuscous; head, pronotum, thoracic

[9] For complete synonymy see: 1953. *Buenoa antigone antigone* (Kirkaldy); Truxal, Univ. Kansas Sci. Bull., 35 (11): p. 1376.




Figures 33-36. North to south variation in total length. **33.** *Buenoa platycnemis.* **34.** *Buenoa pallens.* **35.** *Buenoa pallipes.* **36.** *Buenoa crassipes.* Abbreviations for localities (at left of each bar): B-NT = Brazil: Nova Teutonia; Co-V = Colombia: Villavieja; CR-C = Costa Rica: Cartago; CR-S = Costa Rica: Sarapiqui; CR-SJ = Costa Rica: San José; Cu = Cuba; GC = Grand Cayman; H-T = Honduras: Tela; J = Jamaica; M-C = Mexico: Campeche; M-Mi = Mexico: Michoacan; M-Mo = Mexico: Morelos; M-O = Mexico: Oaxaca; M-S = Mexico: Sonora; Pa-V = Paraguay: Villarrica; Pe-A = Peru: Amazonas; Pe-C = Peru: Cajamarca; Pe-SM = Peru: St. Martin; PR = Puerto Rico; SC = St. Croix; ST = St. Thomas; US-F = United States: Florida; US-T = United States: Texas. Numbers at right of each bar indicate the number of specimens studied.

venter and limbs testaceous. Scutellum brown to black with apex light. Abdomen black, except for ventral keel and portions of conexivum.

*Male structural characters.* — Outline of head laterally rounded when viewed from above. Greatest width of head about five times the width of vertex. Synthlipsis approximately one-half the width of vertex. Tylus not inflated; rostral prong originating at basal portion of third rostral segment. Fore femur thickened at apex and with a triangular stridulatory area consisting of about thirty-five ridges. Genital claspers normal.

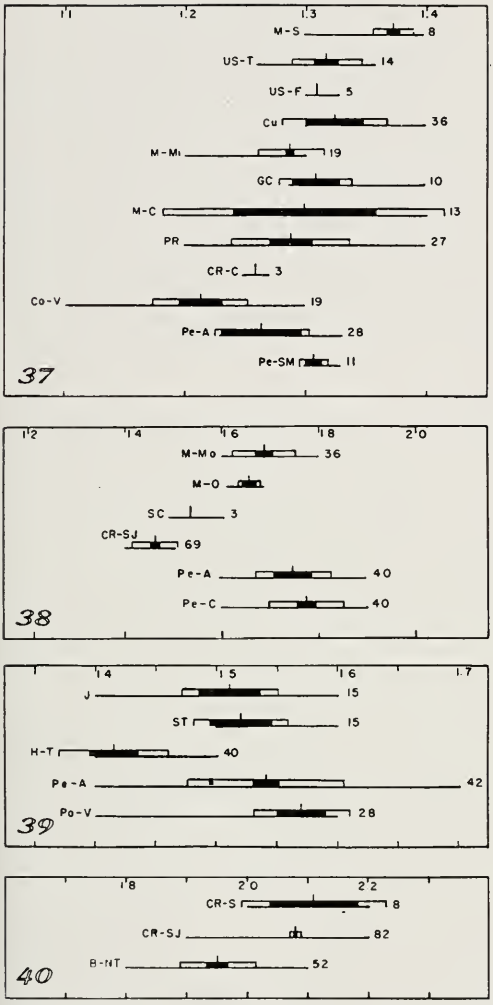
*Female structural characters.*—Head shaped as in males, about five and one-half times width of vertex. Synthlipsis as in males. Pronotum with disc unimpressed. Scutellum large, with median length greater than that of pronotum. Ovipositor normal in shape, with teeth in two rows, and inner one of few large teeth and an outer one of smaller teeth.

*Geographic distribution.* — This species has not been reported for Costa Rica, although the recorded geographic distribution suggests its presence. It has been reported for Mexico, Guatemala, and Uruguay.

## IV. Geographic Variation in *Buenoa*

In his revision of the Genus *Buenoa,* Truxal (1953) wrote: "...It is interesting to note that in spite of wide ranges, a striking feature in *Buenoa* is the lack of geographic variation in most specimens studied. There are only three good examples that are obvious. One case is primarily an example of size variation...". He points out that for *B. limnocastoris* and *B. confusa,* there is size variation from a large northern form to a small southern form. This type of clinal variation, known as Bergman's rule, was first reported for mammals (Bergman, 1847). Some other insects have been found to follow this pattern of geographic variation (Hubbell, 1956), but the number of forms studied and their geographic ranges are too small to permit generalizations in this respect.

The geographic range studied by Truxal is from Manitoba in Canada to Florida. Although his studies seem to be conclusive there were questions not yet answered: Is this north-to-south variation true for neo-




Figures 37-40. North to south variation in head width. **37.** *Buenoa platycnemis.* **38.** *Buenoa pallens.* **39.** *Buenoa pallipes.* **40.** *Buenoa crassipes.* Abbreviations same as in figures 33-36.

tropical forms? Is it also true for measurements other than total length? There is also another question that, as far as I know, has not been answered for insects: Is a reversal of this rule expected once the equator is reached? A report (Hesse et al, 1937) on variations of penguins south of the equator, gives weight to this presumption since birds also follow Bergman's rule.

To answer these questions, 717 specimens of four species of *Buenoa,* which are represented in Costa Rica, were selected for study because of their wide geographic distribution. The species are: *B. pallens* (ranging from Oaxaca, Mexico to Celendin, Peru), *B. pallipes* (from St. Thomas to Villarica, Paraguay), *B. platycnemis* (from Sonora, Mexico to San Martin, Peru) and, *B. crassipes* (from Heredia, Costa Rica to Nova Teutonia, Brazil).

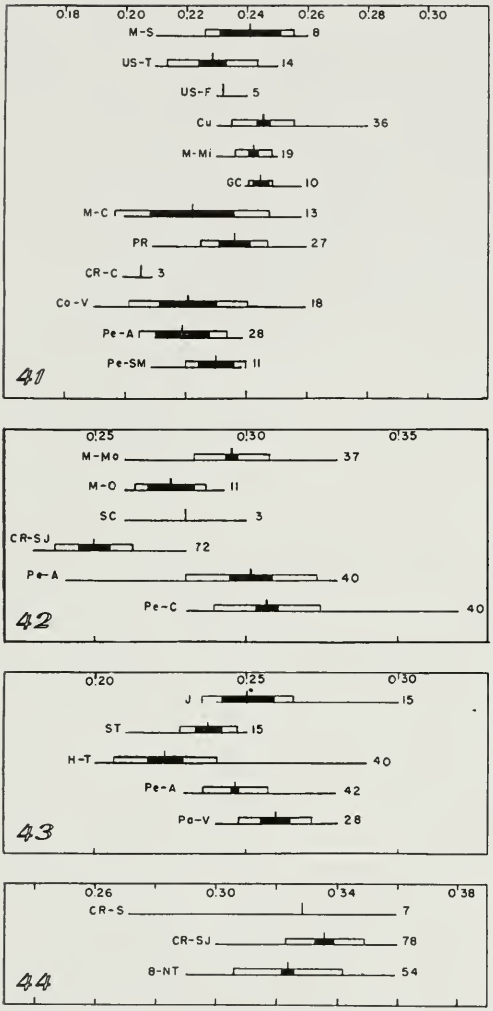
In all specimens, four measurements were taken: total length, head width, vertex width, and width of synthlipsis. These measurements are used in the taxonomy of the group, hence checking their variability was of great interest. The populations studied were grouped according to the states or provinces of origin, except for the island countries where the reduced territorial extension and environmental homogeinity did not justify territorial subdivisions.

*Total length.*—Figures 33-36 show variation in total length for the four species studied. *B. platycnemis* (fig. 33) has a tendency to diminish in size from north to south, with a clear inversion of this trend once the equator is passed. Except for the populations from Florida and Michoacan, there is no variation to be expected. *B. pallens* (fig. 34) follows the rule without any deviation, showing also inversion south of the equator. In *B. pallipes* (fig. 35), there is also a reduction in size from north to south. The inversion south of the equator is not evident in one case: Villarica, Paraguay. The same is also true for *B. crassipes* (fig. 36), with one population south of the equator not following the expected trend.

*Head width.*—For *B. platycnemis* (fig. 37) the expected comes true, with inversion south of the equator. The few deviations are not significant. *B. pallens* (fig. 38) and *B. pallipes* (fig. 39) also follow the expected pattern, showing inversion below the equator. And again, *B. crassipes* (fig. 40) is the one that, although with a clear north to south variation, does not follow the south of the equator inversion.

*Vertex width.*—*B. platycnemis* (fig. 41), *B. pallens* (fig. 42), *B. pallipes* (fig. 43) and *B. crassipes* (fig. 44), show reduction in size of head width from north to south. There is only one minor, insignificant, deviation for *B. pallens.* The inversion south of the equator is also clear in all cases but *B. crassipes.*

*Synthlipsis width.*—*B. platycnemis* (fig. 45) has a general trend in diminishing this

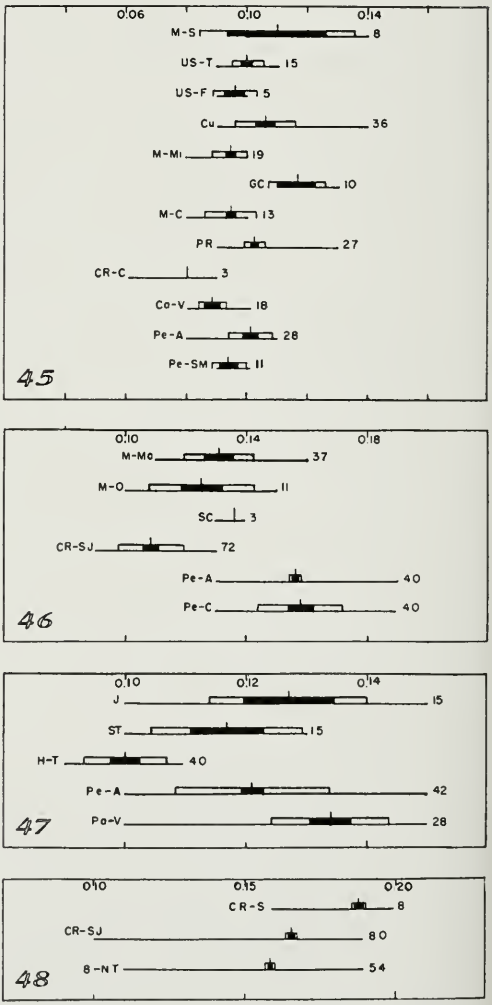



Figures 41-44. North to south variation in vertex width. **41.** *Buenoa platycnemis.* **42.** *Buenoa pallens.* **43.** *Buenoa pallipes.* **44.** *Buenoa crassipes.* Abbreviations same as in figures 33-36.

measurement from north to south, but shows deviations for three island populations: Cuba, Grand Cayman, and Puerto Rico. *B. pallens* (fig. 46) follows the expected variation, except for an island population (St. Croix), also showing inversion south of the equator. *B. pallipes* (fig. 47) and *B. crassipes* (fig. 48) are clear in their north to south variation, but the latter does not have inversion below the equatorial line.

*Discussion and conclusions.*—Clearly, there is a reduction in measurements from north to south, with inversion once the equator is passed. This geographic clinal variation is due to temperature and therefore could be affected by such other factors as seasonal and altitudinal variations. Compensation for these possibilities is not included in the graphs, but should be borne in mind.

For total length, north to south clinal variation is consistent, the exceptions being populations from Florida and Michoacan (*B. platycnemis*). In the first case the sample is too small to be statistically conclusive. The case of Michoacan, I can explain only as a case of seasonal variation.




Figures 45-48. North to south variation in synthlipsis width. **45.** *Buenoa platycnemis.* **46.** *Buenoa pallens.* **47.** *Buenoa pallipes.* **48.** *Buenoa crassipes.* Abbreviations same as in figures 33-36.

The specimens studied were collected during late summer, which could account for their reduced size in spite of the high latitude of Michoacan.

Equatorial inversion for total length is also consistent. Two deviations were found to this: the Paraguay sample for *B. pallipes* and Nova Teutonia, Brazil sample for *B. crassipes*. In both cases the altitude probably caused the deviations; both localities, in spite of being far south of the equator (26° and 27° latitude) are in lowlands with a climate of tropical type similar to the equatorial one.

For head width and vertex width, the actual results were as expected, with the exception of the samples of *B. platycnemis* from three island populations. For these populations, the mean values are above the expected. Local variation, preserved and accentuated by geographic isolation, is the only answer I can give to explain this deviation. Inversion south of the equator is also true except in one case, San Martin, Peru (*B. platycnemis*). I do not have any data on the altitude of this locality and presume it is in lowlands of equatorial type, which would explain the deviation.

More studies on the geographic, altitudinal and seasonal variations are desirable. Our knowledge on the evolution of the notonectids is slight and no doubt the comparative study of populations will be critical in this respect. To date this has not been attempted.

## V. Acknowledgements

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Abstract

The Notonectidae of the Central Plateau of Costa Rica were studied. Six species are reported (*Notonecta c. ceres, N. indica, Buenoa crassipes, B. pallens, B. pallipes, B. platycnemis*), one of them (*N. indica*) is a first record for Costa Rica; five other species (*N. confusa, N. ochrothoe, B. antigone, B. gracilis, B. ida*) from neighboring areas are anticipated. All are included in a key to the Costa Rican species. The life cycle of *N. c. ceres* is described and illustrated. A taxonomic analysis of four populations of *N. c. rogersi* was made showing that this subspecies intergrades with *N. c. ceres* and is here considered synonymous. Growth rates were studied for eight notonectids, the factor 1.3 being considered as the possible growth rate factor for all the members of the family. North to south variation was studied in samples of twenty-six populations of four species of *Buenoa*. Reduction in body measurements was observed from north to south (Bergman's rule), and inversion of this trend was found in populations south of the equator.

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## THREE ASCOCOTYLE COMPLEX TREMATODES (HETEROPHYIDAE) ENCYSTED IN FISHES FROM LOUISIANA, INCLUDING THE DESCRIPTION OF A NEW GENUS

FRANKLIN SOGANDARES-BERNAL
and
JOHN F. BRIDGMAN,
*DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY*
*NEW ORLEANS, LOUISIANA*

## AGE AND GROWTH OF THE SPOT, *LEIOSTOMUS XANTHURUS* LACÉPÈDE

BANGALORE I. SUNDARARAJ,
*DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY,*
*NEW ORLEANS, LOUISIANA*

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# THREE ASCOCOTYLE COMPLEX TREMATODES (HETEROPHYIDAE) ENCYSTED IN FISHES FROM LOUISIANA, INCLUDING THE DESCRIPTION OF A NEW GENUS[1]

FRANKLIN SOGANDARES-BERNAL
and
JOHN F. BRIDGMAN,
*Department of Zoology, Tulane University*
*New Orleans, Louisiana*

Results of preliminary investigations of heterophyid trematodes encysted in littoral poeciliid and cyprinodont fishes from brackish Lake Pontchartrain, Louisiana, are reported. Infected poeciliids and cyprinodonts form a natural source of infection for wading birds and certain mammals which feed on them. At times low intensities of infection in wild adult birds with the *Ascocotyle* complex of species, from areas of heavily infected poeciliid and cyprinodont enzoöicity, show that some immunity (age?) factor may be in operation. Evidence of a presumptive immunity was observed by one of us (F.S.) on the west coast of Florida. Nestling birds believed to be about from one to four days old sometimes had a higher intensity of infection with *Ascocotyle* complex species than their parents. Exposure of cercariae of the *Ascocotyle* complex of species, when these are known, to sera from naturally infected nestling and adult birds may produce interesting results.

The broad spectrum of definitive hosts of *Ascocotyle* complex species, coupled with the modern reappearance of uncooked exotic dishes, may eventually cause these trematodes to be of public health importance in this country.

Acknowledgements are extended to Mr. C. W. Philpott, and Dr. B. I. Sundararaj, of our department, for aid in collecting fish intermediate hosts.

Unless otherwise specified, all measurements are in millimeters.

1. *Ascocotyle leighi* Burton, 1956

*Second intermediate host in Louisiana.*—*Mollienisia latipinna* LeSueur, sail-fin molly (family Poeciliidae).

*Location.*—In lumen of conus arteriosus and lumen and wall of ventricle of heart.

*Locality of second intermediate host.*—West end of U. S. Highway 11 Causeway, south shore of Lake Pontchartrain, Louisiana; new locality record.

*Discussion.*—Burton (1956) described this species from specimens collected from the conus arteriosus of *Mollienisia latipinna* in Florida. He was able to obtain gravid adults from experimental infections in chicks, but was unable to observe the flame cell pattern which in our specimens is $2[(2+2)+(2+2)]$.

Price (1936) sectioned specimens of *Ascocotyle megalocephala* Price, 1932, but did not report a membrane surrounding the muscular oral appendage of this species. Metacercariae of *Ascocotyle leighi* collected from the heart of *Mollienisia latipinna* from Lake Pontchartrain, Louisiana, were examined microscopically for details of the muscular oral appendage. This appendage seems to be surrounded by a thin, well defined, membrane which is continuous with at least the basal portion of the oral sucker. This membrane is not apparent in whole mounts stained with Delafield's hematoxylin and can best be observed in live material when the tip of the appendage is contracted. When the appendage is relaxed, the surrounding membrane seems to stretch and adhere so closely to the appendage that it is difficult to observe. The overlap of the muscular oral sucker appendage with the pharynx varies as has been clearly pointed out by Martin (1953) and Stunkard and Uzmann (1955) for *Parascocotyle lageniformis* and *Parascocotyle diminuta* respectively. Prolonged observations of *Ascocotyle leighi* metacercariae, under slight coverslip pressure, revealed that the extension of the forebody did not always control the length of the muscular oral appendage. Variation in position of the appendage is due to extension of the appendage as well as contraction of the forebody which in turn

[1]This investigation was supported in part by a grant (G-13000) from the National Science Foundation.

shortens the distance between the pharynx and oral sucker. The latter factor seems to be the major cause of variation.

The ventrogenital sac wall of metacercariae of *Ascocotyle leighi* varies in shape. Live metacercariae were observed, under a floated coverslip, to orient the acetabular concavity anteriorly and to clasp the wall of the ventrogenital sac. Repeated observations revealed that this acetabular sucking action modified the shape of the ventrogenital sac wall. Perhaps acetabular manipulations occasionally serve the purpose of ejecting eggs from the ventrogenital sac in gravid worms.

The gonotyl of *Ascocotyle leighi* is as pictured by Burton (1956). The gonotyl fills most of the ventrogenital sac and appears to be provided, when live material is studied under 1,250X magnification, with a patch of very minute spines on its ventral surface adjacent to the ventrogenital sac membrane. The gonotylar spines are not visible in specimens stained with Delafield's hematoxylin.

### 2. *Parascocotyle diminuta* Stunkard and Haviland, 1924 (Figure 1)

*Second intermediate hosts in Louisiana.*—*Cyprinodon variegatus* Lacépede, broad killfish, *Fundulus grandis* (Baird and Girard), chub; *Fundulus jenkinsi* (Evermann), chub; *Lucania parva* (Baird and Girard), rain water fish (family Cyprinodontidae); and *Mollienisia latipinna* LeSueur, sailfin molly (family Poeciliidae); all new host records.

*Location.*—Gill filaments of all hosts.

*Locality.*—West end of U. S. Highway 11 Causeway, south shore of Lake Pontchartrain, Louisiana; new locality record.

*Discussion.*—*P. diminuta* reported here appears to be the same species reported by Stunkard and Uzmann (1955).

Stunkard and Haviland (1924) named and described *Parascocotyle diminuta* from rats collected at Clason Point, New York. Their specimens had lost some of the oral spines. Later Stunkard and Uzmann (1955) studied the partial life history of a trematode that they believed to be *Parascocotyle diminuta.* The metacercariae were found in naturally infected *Fundulus heteroclitus* (Linn.) and *Fundulus majalis* (Walbaum) collected on the northeastern coast of the United States. Specimens of *F. heteroclitus* from the *P. diminuta* type locality were examined by these authors and were found infected with metacercariae that were identified as *P. diminuta.* Stunkard and Uzmann (1955) did not mention the establishment of experimental infections of definitive hosts with *P. diminuta* metacercariae collected at the type locality. We assume that the metacercarial cysts studied by these authors were at least dissected, and oral spination and other morphological details observed. The occurrence of intermediate hosts infected with *Parascocotyle* metacercariae at the type locality lend support to the hypothesis that the species which Stunkard and Uzmann (1955) reported is *Parascocotyle diminuta* on epizootiological grounds. Hutton and Sogandares (1958) followed the description of Stunkard and Uzmann (1955) when they identified egg-producing adult specimens of *P. diminuta* obtained from a hamster experimentally exposed to metacercariae from the gills of *Fundulus similis* (Baird and Girard) collected in the vicinity of St. Petersburg, Florida. On physiological and morphological bases, the identification of *P. diminuta* by Hutton and Sogandares (1958) is in accordance with evidence presented by Stunkard and Uzmann (1955). These latter authors were able to obtain gravid adults of *P. diminuta* from rats and hamsters though not from mice or chicks. Chicks proved to be refractory to infection. Specimens of *P. diminuta* from *Mollienisia latipinna* in Louisiana produced eggs in a mouse but not a hamster. Martin (1953) studied the partial life-history of a trematode that he believed was identical with *Parascocotyle lageniformis* (Chandler, 1941). He collected metacercariae from the gills of *Fundulus pallidus* Evermann in Texas, and obtained gravid adults from experimental infection of chicks. Although Stunkard and Uzmann (1955) reported chicks refractory to infection with *P. diminuta,* they did not state the age or food of the chicks. As is well known new-born chicks are sometimes more susceptible to trematode infections than are older ones. Furthermore, experimental infections of older chicks are sometimes dependent upon diet. Thus, at present we cannot evaluate the physiological

host-specificity of the two species reported by these authors. Chandler (1941) and Martin (1953) could not have known the details of the oral spination of *P. diminuta* since it was not until 1955 that Stunkard and Uzmann redescribed the species. On morphological grounds there is little doubt that *P. diminuta* Stunkard and Haviland, 1924, and *P. lageniformis* (Chandler, 1941) are identical. All meristic and morphological characters of the two species appear to overlap. The possibility of morphologically identical physiological strains or species precludes a definite stand regarding the synonymy at this time. We are in agreement with Martin (1953) that *Phagicola nana* (Ransom, 1921) of Byrd and Reiber (1942) from a Louisiana muskrat is probably *P. lageniformis,* and thus is possibly conspecific with *P. diminuta.* Poeciliid and cyprinodont fishes are frequently found living in the same brackish marshes with muskrats in the New Orleans area. Another view is that *P. diminuta* of Stunkard and Uzmann, 1955, is in reality *Parascocotyle lageniformis* (Chandler, 1941) and that the taxon *Parascocotyle diminuta* Stunkard and Haviland, 1924, is a different species. This last possibility is cautiously not subscribed to here. This doubt will always remain because the type material of *P. diminuta* lacks a complete set of oral spines.

Stunkard and Uzmann (1955) reported experimental infections of laboratory-raised *Larus argentatus* (Linn.) and *Nycticorax nycticorax* (Linn.). These authors did not state whether their *Larus* specimen was hatched in the laboratory. One of us (F.S.) found a large percentage of several species of coastal birds with estimated ages of one to four days, infected with trematodes due to feeding of infected food material by their mothers. The *Nycticorax* apparently infected by Stunkard and Uzmann was a young female captured in Bronx Park, New York. Thus, we do not know if Stunkard and Uzmann actually infected their birds experimentally. The fact remains that these hosts were found infected with *P. diminuta.* Price (1933) reported *P. diminuta* from Butorides. Hutton and Sogandares (1960) reported *P. diminuta* from naturally infected *Phalacrocorax auritus floridanus* (Audubon) and *Hydranassa tricolor ruficollis* (Gosse) in Florida. To this list we now add *Nycticorax nycticorax hoactli* (Gmelin) and *Procyon lotor* (Linn.) from the west coast of Florida. Mr. Larry Ash, Department of Parasitology, Tulane University, has also given us some specimens of *P. diminuta* collected from a racoon in Louisiana. Thus *P. diminuta* appears to be a polyxenous parasite known to occur naturally in at least two or possibly three unrelated mammals and five or possibly six birds. *P. diminuta* populations from different localities may prove to have developed into "strains" which are identifiable only on a physiological basis. The possibly many faceted physiological host-specificity of *P. diminuta* metacercariae from different intermediate hosts and localities is being investigated further in this laboratory.

Metacercariae of *P. diminuta* collected by us were observed alive under slight coverslip pressure. Cysts in the gill filaments of *Fundulus jenkinsi* (fig. 1) were 0.136 to 0.200 long and were oval in shape. Cysts from the gills of *Mollienisia latipinna* were 0.200 to 0.201 long by 0.119 to 0.144 wide. The surrounding cyst membranes, gonotyl spination, and flame cell pattern ($2\,[(2+2)+(2+2)]$) are as reported by Stunkard and Uzmann (1955). Mechanically excysted metacercariae have respectively 16 and 2 oral spines in one complete and an incomplete dorsal accessory row. Metacercariae of *P. diminuta* from different intermediate hosts in Louisiana possessed a constant number and arrangement of oral spines.

### 3. **Pseudascocotyle mollienisicola,** n. gen., n. sp.
(Figures 2-4)

*Second intermediate host in Louisiana.*—*Mollienisia latipinna* LeSueur, sailfin molly (family Poeciliidae).

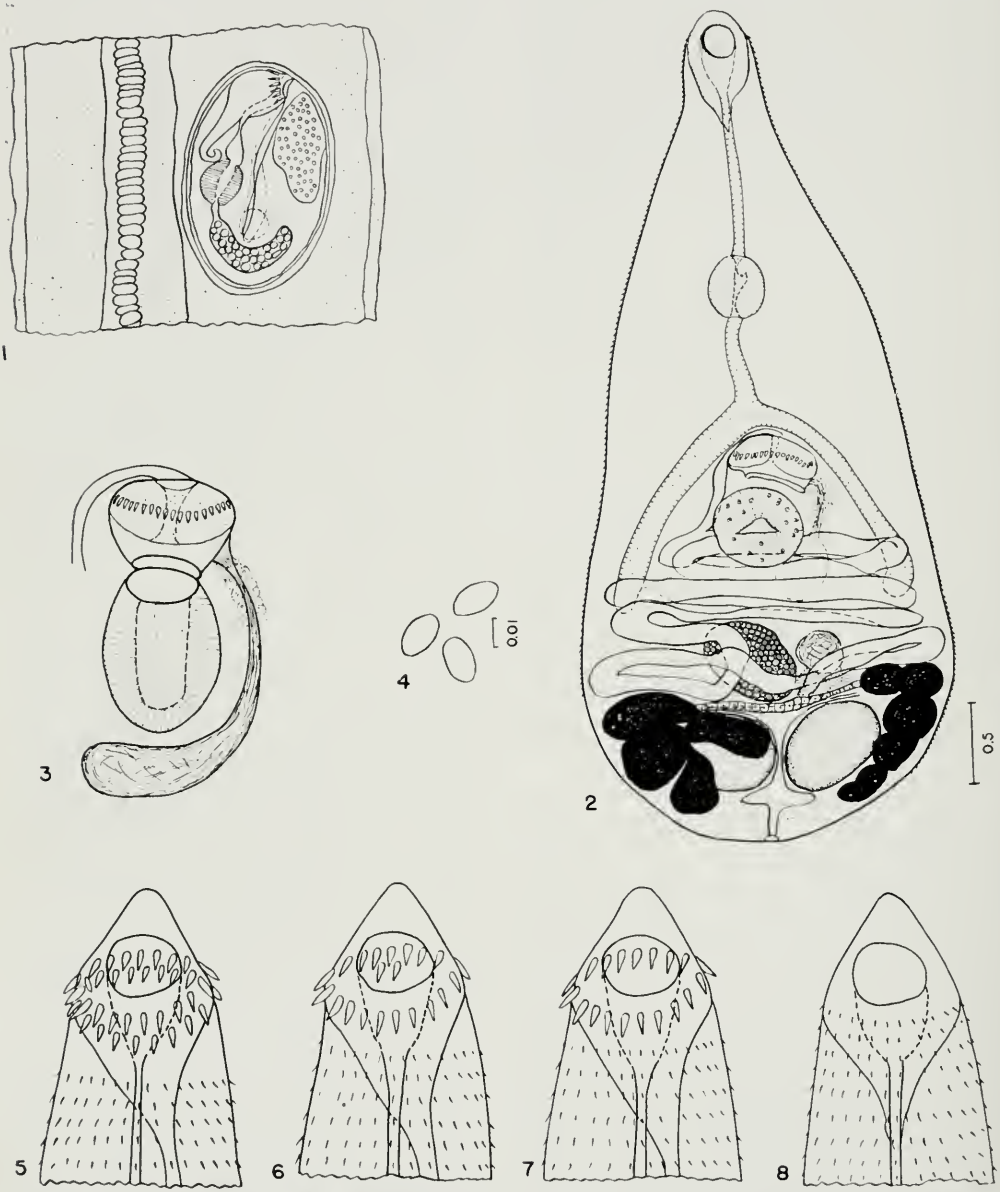
*Location.*—Encysted on wall and surface of intestine, body musculature, and on gill branchiae.

*Locality of second intermediate host.*—West end of U. S. Highway 11 Causeway, south shore of Lake Pontchartrain, Louisiana.

*Holotype.*—U. S. Nat. Mus. Helm. Coll. No. 39446.

*Diagnosis* (measurements on 3 gravid specimens, obtained from an experimental hamster infection, killed in boiling water).—Body flattened dorsoventrally, pyriform in outline, 0.476 to 0.527 long by 0.221 to

0.255 wide. Forebody 0.255 to 0.289 long. Cuticle completely spined to level of testes. "Eyespots" present in region of prepharynx and or pharynx. Oral sucker terminal, with a rudimentary muscular appendage, lacking oral spines; 0.036 to 0.036 wide by 0.056 to 0.056 from anterior end of sucker to posterior tip of muscular appendage. Pre-




Figures 1-8. **1.** *Parascocotyle diminuta;* metacercaria encysted in gill filament of *Fundulus jenkinsi.* **2.** *Pseudascocotyle mollienisicola,* sp. nov., ventral view. **3.** Same; terminal genitalia and acetabulum oriented anteriorly along longitudinal axis of body. **4.** Same; uterine eggs. **5.** *Ascocotyle, sensu stricto;* representative oral and cuticular spination. **6.** *Parascocotyle, sensu stricto;* representative oral and cuticular spination. **7.** *Phagicola, sensu stricto;* representative oral and cuticular spination. **8.** *Pseudascocotyle, sensu stricto;* representative cuticular spination.

Unless otherwise specified, all drawings were made with the aid of a camera lucida. The projected scales have the value in millimeters.

pharynx inserting ventral to muscular appendage of oral sucker; 0.088 to 0.100 long, or about 1.57 to 1.78 times longer than oral sucker, depending upon contraction of forebody. Pharynx 0.040 to 0.048 long by 0.040 to 0.040 wide. Esophagus from 0.044 to 0.052 long, depending upon contraction of forebody. Ceca 2, connecting with esophagus, one on each side of body, extending a short distance posterior to acetabulum. Acetabulum 0.048 to 0.048 long by 0.056 to 0.056 wide. Sucker width ratio about 1:1.4.

Ventrogenital pore median followed by a ventrogenital sac with a gonotyl about 0.012 to 0.016 long by 0.044 to 0.048 wide at its anterior border. Gonotyl with a ventral set of 17 conspicuous spines arranged equatorially in a transverse row. Testes 2, in posterior ¼ body, side by side; sinistral testis 0.048 to 0.064 long by 0.048 to 0.072 wide; dextral testis 0.064 to 0.064 long by 0.056 to 0.076 wide. Seminal vesicle saccular, extending from a short distance posterior to acetabulum to insert on sinistral side of ventrogenital sac at level of posterior border of gonotyl where it is surrounded by prostate cells. Ovary between acetabulum and testes, displaced to right of body midline; oval in shape, 0.056 to 0.076 long by 0.068 to 0.076 wide. Seminal receptacle equatorial and sinistral to ovary. Mehlis' gland amid ovary, seminal receptacle, and sinistral testis. Oviduct (visible in live metacercariae) ciliated. Vitelline glands of coarse follicles, usually dorsal and ventral to outer aspect of testes, extending from behind testes to level of ovary. Vitelline duct between testes and ovary, expanding to form a small vitelline receptacle at level of Mehlis' gland. Uterus in transverse coils, restricted between testes and cecal bifurcation, approaching ventrogenital sac on dextral side to insert into anterior border where it perforates the gonotyl to open on its median posterior border as a uterine pore. Eggs (fig. 4) 0.016 to 0.020 long by 0.012 to 0.012 wide. Excretory vesicle extending from a median posterior excretory pore, between testes, usually following their contour, to end on anterior aspect of testes; excretory ducts branching at level of or slightly anterior to acetabulum; flame cell formula 2 [(2 + 2) + (2 + 2)].

*Generic diagnosis of Pseudascocotyle.*— Small heterophyid trematodes with a dorsoventrally flattened pear-shaped body. "Eyespots" present. Cuticle spined. Oral sucker terminal, lacking spines, with a rudimentary muscular appendage. Prepharynx, pharynx, and esophagus present. Ceca 2, one on each side of body, terminating a short distance posterior to equator. Acetabulum present. Ventrogenital pore immediately anterior to acetabulum, followed by an anteriorly directed ventrogenital sac bearing, on its anterior portion, a prominent gonotyl which is transversely spined at its equator. Testes 2, side by side, in posterior end of body. Seminal vesicle non-muscular, saccular, extending from a short distance behind acetabulum to insert sinistrally on ventrogenital sac at level of posterior border of gonotyl; surrounded by prostate cells at junction with ventrogenital sac. Ovary between acetabulum and testes, slightly displaced to right of body midline. Seminal receptacle adjacent and sinistral to ovary. Mehlis' gland amid ovary, seminal receptacle, and sinistral testis. Oviduct ciliated (in metacercaria). Vitelline glands composed of coarse follicles, extending from behind testes to level of ovary, overlapping testes dorsally and ventrally on their anterior course; vitelline reservoir at level of Mehlis' gland. Uterus confined between pretesticular area and cecal bifurcation, approaching ventrogenital sac on its dextral side, entering sac anteriorly where it penetrates the gonotyl to open on its median posterior border. Eggs small, thin shelled. Excretory vesicle extending from terminal excretory pore, intertesticular, usually following contour of testes on its anterior extent, to end on anterior aspect of testes; excretory ducts branching in region of acetabulum; flame cell formula 2[(2 + 2) + (2 + 2)].

*Type species.*— *Pseudascocotyle mollienisicola.*

*Discussion.*— The genus *Pseudascocotyle* is most closely related to the heterophyid genera *Ascocotyle* Looss, 1899, *Phagicola* Faust, 1920, and *Parascocotyle* Stunkard and Haviland, 1924, but differs by possessing a gonotyl that is perforated by the uterus, and by lacking oral spines. *Pseudascocotyle* seems to be most closely related to *Phagicola* and *Parascocotyle* in that the vitellaria extend to the level of the ovary.

The lack of oral spines in *Pseudascocotyle*

was at first believed to represent an artifact when adults were removed from an experimental hamster infection. Studies of the metacercariae soon removed these doubts. Cuticular spines, which in most species of *Ascocotyle, Phagicola,* and *Parascocotyle* begin a short distance posterior to the crown spines, leaving a bare zone, extended almost to the oral sucker aperture in our specimens of *Pseudascocotyle.* We have not made an exact count of sailfin mollies found infected but the incidence is high, at least 95 percent. Sailfin mollies of 23 mm total length were infected.

The following artificial key will serve to separate the four genera of the Ascocotylinae Yamaguti, 1958, as we presently visualize the subfamily.

1. Oral sucker with one or more circlet(s) of spines (figs. 5 to 7); vitellaria extending either to level of ovary or to acetabulum ..... 2
   Oral sucker lacking spines (fig. 8); vitellaria extending to level of ovary ..... *Pseudascocotyle,* (this paper)
2. Oral sucker with two complete circlets of spines (fig. 5); vitellaria usually extending to level of acetabulum ..... *Ascocotyle, sensu stricto*
   Oral sucker never with two complete circlets of spines (figs. 6 to 7); vitellaria never extending to acetabulum ..... 3
3. Oral sucker with a single complete circlet of spines and an incomplete accessory dorsal row of from 2 to 4 spines (fig. 6); vitellaria extending to level of ovary ..... *Parascocotyle, sensu stricto*
   Oral sucker with a single complete circlet of spines (fig. 7); vitellaria extending to level of ovary ..... *Phagicola, sensu stricto*

## The *Ascocotyle* Complex

The heterophyid trematodes of the genera *Ascocotyle* Looss, 1899, *Phagicola* Faust, 1920, *Parascocotyle* Stunkard and Haviland, 1924, and *Pseudascocotyle* (this paper) are collectively known as the *Ascocotyle* complex. Species of the *Ascocotyle* complex were placed in the heterophyid sub-families Centrocestinae Looss, 1899, by Price (1940) and Ascocotylinae Yamaguti, 1958, by Yamaguti (1958), though the premetacercarial stages are unknown.

The status of the various genera or subgenera of *Ascocotyle* complex species has been much disputed by several recent authors. At least three different views have developed in connection with generic or sub-generic designation of the species groups. Price (1932, 1936) retained the forms with two complete rows of oral spines in the genus *Ascocotyle.* He reserved the genus *Phagicola* for those species with a single and/or second dorsal incomplete row of oral spines. This view seemingly received support from Martin (1951, 1953) and others. Stunkard and Uzmann (1955) reviewed the literature concerning *Ascocotyle* complex species, and maintained that *Parascocotyle* is a synonym of *Phagicola* and that the latter is a subgenus of *Ascocotyle.* Yamaguti (1958) disregarded the number of rows of oral spines and relied upon a character that almost always coincides with oral spination, the anterior vitelline extent, to separate *Ascocotyle* from *Phagicola.* According to Yamaguti (1958), Parascocotyle is a synonym of *Phagicola.* Burton (1958) recognized *Ascocotyle* and *Phagicola.* Almost simultaneously with the appearance of Yamaguti's volume I (1958), Hutton and Sogandares (1958) arrived at conclusions somewhat similar to his except for regarding *Parascocotyle* a valid genus. Hutton and Sogandares (1958, 1959) used the anterior vitelline extent only to separate *Ascocotyle* from *Phagicola* and *Parascocotyle.* The use of the anterior vitelline extent was nothing new since Witenberg (1929) had used this character to separate *Parascocotyle* from *Ascocotyle.* Witenberg considered *Phagicola* a synonym of *Parascocotyle,* but Price (1932) clearly pointed out that *Phagicola* has date priority. From the systematic point of view there appear to be four species groups in the *Ascocotyle* complex. *Ascocotyle angeloi* Travassos, 1928, possesses intergrading characters (2 complete rows of oral spines and vitellaria to ovary) between *Ascocotyle, sensu stricto,* (forms with 2 complete rows of oral spines and vitellaria usually extending to level of acetabulum), *Phagicola, sensu stricto,* (forms with 1 complete row of oral spines and vitellaria extending to level of ovary), *Parascocotyle, sensu stricto* (forms with one com-

plete row plus one incomplete dorsal accessory row of oral spines and vitellaria extending to level of ovary), and *Pseudascocotyle* (forms lacking oral spines and vitellaria extending to level of ovary). Within a phylogenetic scheme, *A. angeloi* would tend to reinforce the closeness of relationship between *Ascocotyle, Phagicola, Parascocotyle,* and *Pseudascocotyle.* Another view is that *Ascocotyle, Phagicola, Parascocotyle,* and *Pseudascocotyle* are sub-genera of *Ascocotyle.*

Schiller (1957) X-irradiated eggs of *Hymenolepis nana* (Siebold, 1852) to demonstrate that the rostellar hooks of this cestode seem to be a stable meristic character. Possibly this stability may apply to the oral spines of certain trematodes under normal conditions. Examinations of several hundred specimens of certain *Ascocotyle* complex species by one of us (F.S.) seems to bear out this point. Wolfgang (1955) did not find a stability of numbers or number of rows in the oral spines of the acanthocolpid trematode *Stephanostomum baccatum* (Nicoll, 1907) from several hosts in Canada. This variation observed by Wolfgang (1955) possibly may be attributed to a study of worms from abnormal hosts or from superinfections, though he does not make clear the hosts and the intensities of infections from which the abnormal trematodes were taken. Such great variations in oral sucker spination certainly have not been observed by one of us (F.S.) in many specimens of several *Stephanostomum* species collected in the tropical American Atlantic and Pacific.

The structure of the terminal genitalia of *Ascocotyle* complex species has not been used as a device to separate species groups. The terminal genitalia have rarely been described in detail because these structures are difficult to observe even with the best optical equipment. The gonotyl of *Ascocotyle* complex species is variable in spination, shape, and structure. The gonotyl may possess spines or refractile chitin-like bars. These spines or bars are difficult to observe in stained whole mounts, though they are rather easily observed in live specimens. Apparently no spines or bars have been previously reported from the gonotyl of species of *Ascocotyle sensu stricto.* Metacercariae of *Ascocotyle leighi* Burton, 1956, from the heart of *Mollienisia latipinna* Le Sueur in Louisiana, *Parascocotyle diminuta* Stunkard and Haviland, 1924 from the gills of *Fundulus similis* (Baird and Girard) in Florida, *Fundulus jenkinsi* (Evermann), *Fundulus grandis* (Baird and Girard), *Lucania parva* (Baird and Girard), and *Cyprinodon variegatus,* Lacepede in Louisiana, and *Phagicola longa* (Ransom, 1920) from the pericardial membrane of *Mugil cephalus* Linn. and *Mugil curema* Cuv. and Val. in Florida, were observed for details of the gonotyl. As previously mentioned, very fine gonotyl spines appeared to be present in the gonotyl of *Ascocotyle leighi. Parascocotyle diminuta* possess gonotylar spines as reported by Stunkard and Uzmann (1955). The gonotyl of *Phagicola longa* possesses chitin-like bars or rodlets. The gonotyl of *Pseudascocotyle* (this paper) has been described above. The gonotyl of *Ascocotyle, Phagicola,* and *Parascocotyle* is apparently not perforated by the terminal genital ducts, whereas the uterus appears to perforate the gonotyl of *Pseudascocotyle.*

*Ascocotyle* complex species have one detail in common; they all possess a characteristic muscular oral sucker appendage that is not found in other heterophyid trematodes. The flame cell pattern of the metacercariae of certain *Ascocotyle, Phagicola, Parascocotyle,* and *Pseudascocotyle,* species which we have observed in Florida and Louisiana is 2[(2 + 2) + (2 + 2)]. This flame cell pattern corresponds with that of *Centrocestus armatus* (Tanabe, 1922) and *Centrocestus formosanus* (Nishigori, 1924) as reported by Yamaguti (1938) and Martin (1958) respectively. *Centrocestus* Looss, 1899 is the type genus of the Centrocestinae Looss, 1899. Other Centrocestinae with a flame cell pattern of 2[(2 + 2) + (2 + 2)] include the genera *Pygidiopsis* Looss, 1907 and *Pygidiopsoides* Martin, 1951. Martin (1951) included *Caimanicola* Freitas and Lent, 1938 and *Lacerdaia* Travassos, 1931 in the Centrocestinae although Price (1940) had previously pointed out that the genus *Caimanicola* is a synonym of *Acanthostomum* Looss, 1899 (family Acanthostomidae Poche, 1926). One of us (F.S.) agrees with this synonymy, having examined 2 immature specimens of what appears to be the same species collected from the type host, *Caiman sclerops* Gray, in Pirre River, Darien

Province, Panama. The genus *Lacerdaia* apparently is related to *Pygidiopsis* and *Pygidiopsoides,* though a further study of the terminal genitalia of the first would be necessary to evaluate this point. We do not agree with Yamaguti (1958) in establishing a new subfamily for *Pygidiopsis,* and in placing *Pygidiopsoides* in the Haplorchinae Looss, 1899, and *Lacerdaia* in the Opisthometrinae Yamaguti, 1958. Everything we presently know about these genera seems to indicate that they are closely related. Until further studies prove otherwise, we shall retain the subfamily Centrocestinae for those genera (*Centrocestus* Looss, 1899, *Pygidiopsis* Looss, 1907, *Pygidiopsoides* Martin, 1951, and *Lacerdaia* Travassos, 1931) possessing an oral sucker without a muscular appendage and shall tentatively allocate the entire *Ascocotyle* complex of species to the Ascocotylinae Yamaguti, 1958. The Ascocotylinae are similar to the Centrocestinae, though differ in details of terminal genitalia and mainly by possessing an oral sucker with a muscular appendage. If a muscular appendage is found on the oral sucker of cercariae of *Ascocotyle* complex species, it would at present appear to further strengthen the concept of a separate subfamily for this group of species. The cercariae of *Ascocotyle* complex species may be of the opthalmopleurolophocercous type with an oral sucker bearing a reduced muscular appendage, a non-cellular excretory vesicle, a flame cell pattern of $2[(2+2)+(2+2)]$, and a number and arrangement of oral spines characteristic of the genus and species represented.

## Summary

1. The following heterophyid (Ascocotylinae Yamaguti, 1958) trematodes are reported for the first time from Louisiana: *Ascocotyle leighi* Burton, 1956; *Parascocotyle diminuta* Stunkard and Haviland, 1924; and *Pseudascocotyle mollienisicola* (this paper).

2. New second intermediate host records include: *Parascocotyle diminuta* in *Cyprinodon variegatus* Lacepede, *Fundulus grandis* (Baird and Girard), *Fundulus jenkinsi* (Evermann), *Lucania parva* (Baird and Girard) (family Cyprinodontidae); and *Mollienisia latipinna* Le Sueur (family Poeciliidae).

3. Additional anatomical details of *Ascocotyle leighi* encysted in the type host, *Mollienisia latipinna* Le Sueur from Louisiana, are described. These include the apparent presence of a patch of very minute spines on the ventral aspect of the gonotyl proximal to the ventrogenital sac, and a flame cell pattern of $2[(2+2)+(2+2)]$.

4. A new genus, *Pseudascocotyle,* is named for the new species *P. mollienisicola* found encysted in *Mollienisia latipinna. Pseudascocotyle* differs from other genera in the Ascocotylinae Yamaguti, 1958, by lacking oral spines in both the metacercariae and adults and by possessing a gonotyl perforated by the uterus.

5. Gravid specimens of *Ascocotyle leighi* and *Pseudascocotyle mollienisicola* were obtained by feeding metacercariae to a laboratory-raised hamster. *Parascocotyle diminuta* developed to maturity and produced eggs in an experimentally infected laboratory mouse but not in a hamster.

6. The present status of the *Ascocotyle* complex of species is discussed and the subfamily Ascocotylinae Yamaguti, 1958 is recognized. We suggest that cercariae of the *Ascocotyle* complex may be of the opthalmopleurolophocercous type with a reduced muscular oral appendage, a non-cellular excretory vesicle, a flame cell pattern of $2[(2+2)+(2+2)]$ and numbers and row(s) of oral spines corresponding to the species represented.

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ABSTRACT

The trematodes *Ascocotyle leighi* Burton, 1956; *Parascocotyle diminuta* Stunkard and Haviland, 1924 and *Pseudoscocotyle mollienisicola* n. gen., n. sp., (Ascocotlyinae: Heterophyidae) were found encysted in poeciliid and cyprinodont fishes from brackish-water Lake Pontchartrain, Louisiana, All trematode species collected represent new locality records. New second intermediate host records include *Parascocotyle diminuta* in *Cyprinodon variegatus* Lacépède, *Fundulus grandis* (Baird and Girard), *Fundulus jenkinsi* (Evermann), *Lucania parva* (Baird and Girard), and *Mollienisia latipinna* Le Sueur. Previously unknown anatomical details are given for *Ascocotyle leighi*. Metacercariae of all species reported were fed to experimental definitive hosts and mature trematodes were obtained. The present status of the Ascocotylinae is discussed.

# AGE AND GROWTH OF THE SPOT, *LEIOSTOMUS XANTHURUS* LACÉPÈDE[1]

BANGALORE I. SUNDARARAJ,
*Department of Zoology, Tulane University, New Orleans, Louisiana*

## Introduction

The spot, *Leiostomus xanthurus,* a common sciaenid fish along the Atlantic and Gulf coasts from Massachusetts to Texas is especially abundant in estuaries and sounds. The commercial fishery is centered in the Chesapeake Bay area and in the Carolinas. Along the coasts of Louisiana and Texas, the spot is not marketed for human consumption to any great extent. Here it is included with trash fish which are used chiefly in making cat and dog food.

The object of the present investigation was to determine the age and growth of the spot in the Lake Pontchartrain area, Louisiana, based on length-frequency polygons, scale, and otolith studies. Otoliths have not been previously used to determine the age of spot.

Previous attempts to determine the age of spot have been based mostly on the interpretation of modes in length-frequency polygons. Welsh and Breder (1923) reported difficulty in reading its scales. Hildebrand and Schroeder (1928) gave a comprehensive account of the life history of the Chesapeake Bay spot and stated that the wide range of length of spot taken throughout the year made determination of growth rate difficult. Pearson (1928) stated that the spawning season for the spot in the Gulf of Mexico extends from late December through March; the peak was reached in January and February. He also reported on the growth and other aspects of the life history. Hildebrand and Cable (1930) described the larval stages. The smallest spot taken at Beaufort, North Carolina was 1.5 mm in total length; it was assumed to be newly hatched. They also stated that the extended spawning season makes for a great variation in sizes and, as a result, the sizes of fish in successive age groups overlap considerably after the second year. Gunter (1938, 1945) reported on the growth and other aspects of the life history of the spot in Texas and Louisiana waters. Townsend (1956) and Pacheco (1957) recently showed that age determination based on scale studies is possible in the spot. Dawson (1958) studied the biology and life history of the spot with special reference to South Carolina.

## Materials and Methods

In this study 1,418 specimens were used. The collections were made at monthly intervals; 354 were collected during July 1953 to May 1954, 145 during January 1955 to September 1955, and 919 during October 1958 to September 1959. The first two series of collections (*viz.,* 1953-54 and 1955) were made in Lake Pontchartrain proper. The 1958-59 collections were obtained from Saw Mill Pass at the Rigolets, lat. 30° 09′N and long. 89° 44′W (fig. 1). Trammel nets, seines, otter trawls, and rotenone were used to collect the specimens.

Seine and trawl samples (Suttkus, Darnell, and Darnell, 1954) indicate that young-of-the-year are more abundant in the shallower areas of the lake during the period February through April. Later in the season young spot frequent deeper parts of the lake and the trawl is a more effective type of collecting gear. Thirteen trawl stations and seven seine stations were established in Lake Pontchartrain (fig. 1). The monthly samples from each station were not large enough to allow a critical comparison of growth rate between various stations.

*Length Measurements.*—Length measurements were made within a few hours after preservation in 10 percent formalin. Total lengths, measured according to the method of Hubbs and Lagler (1947), were used for growth computations throughout this study. For conversion of total length into standard length a ratio of 1:0.816 was computed for specimens from 19 to 49 mm and a ratio of 1:0.773 for specimens from 50 to 270 mm in total length.

*Scale studies.*—Scales used in the determination of age and growth were removed from the left side of each fish below the

[1] Part of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. degree in Zoology at Tulane University, April, 1960.

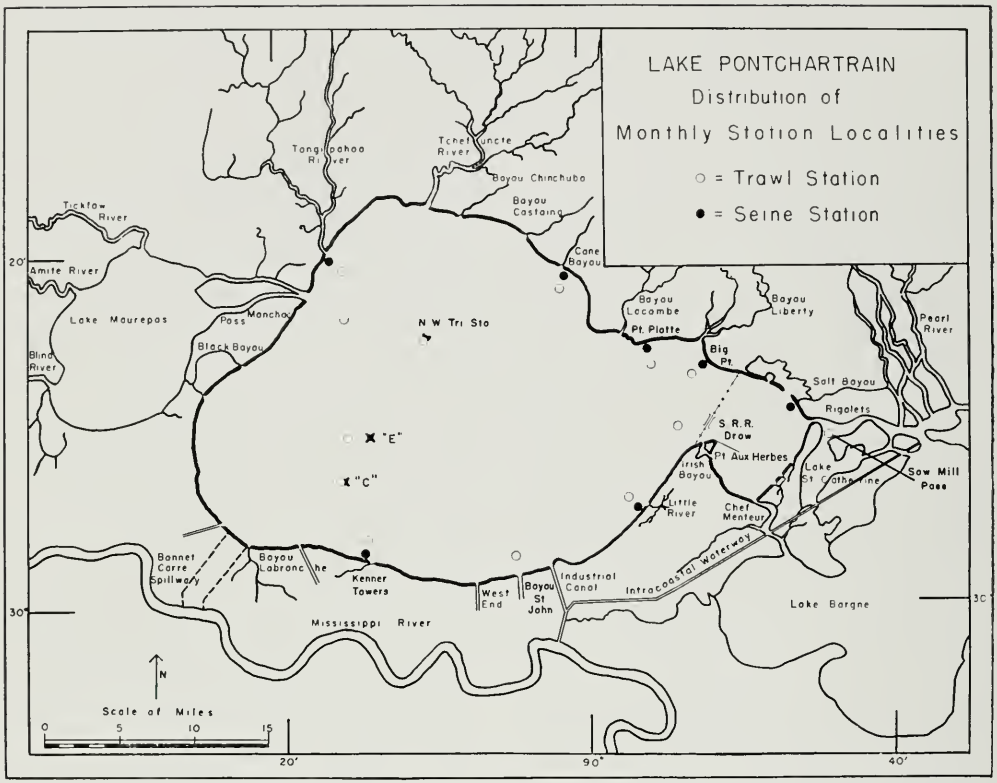



Figure 1. Map of Lake Pontchartrain showing the distribution of monthly trawl and seine stations.

lateral line immediately posterior to the appressed pectoral fin. Regenerated scales were discarded. About 20 scales were removed and rubbed between the fingers to clean off epidermis and slime. The scales were then rinsed in water and stored in scale envelopes. The following information was recorded: total length, date of collection, locality, and method of capture.

In the laboratory, a few scales were removed from each envelope and placed in a 0.5 percent sodium hydroxide solution for a few minutes. Each scale was then cleaned by rubbing between fingers. Impressions of five or six regular scales were made on 3 by 1 inch cellulose acetate strips by use of a roller type press (mfg. William Dixon Inc., Newark, New Jersey). The scale impressions were viewed with a Bausch and Lomb microprojector at a magnification of 57.5 X. Scale images were projected vertically on a sheet of paper. The positions of the projected annuli were marked on strips of paper and these were used for back-calculations. All scales with at least one annulus were read several times until the results were concordant. In addition to the enumeration of annuli, the number of circuli from focus to each annulus and to the anterior margin of the scale were counted.

*Otolith studies.*—A median sagittal incision was made on the head, in a dorsoventral direction. The two resulting halves were forced outwards and both otoliths removed with a forceps. They were stored dry in their respective scale envelopes. Otoliths were removed only from 1955 and 1958-59 samples.

Some authors have emphasized the importance of not allowing the otoliths to become dry while others stored them dry. Spot otoliths did not lose their clarity after four years of dry storage in this laboratory. Ling (1958) stated that the clarity of the sea garfish, *Reporhamphus melanocheir*, otoliths did not suffer from the effects of

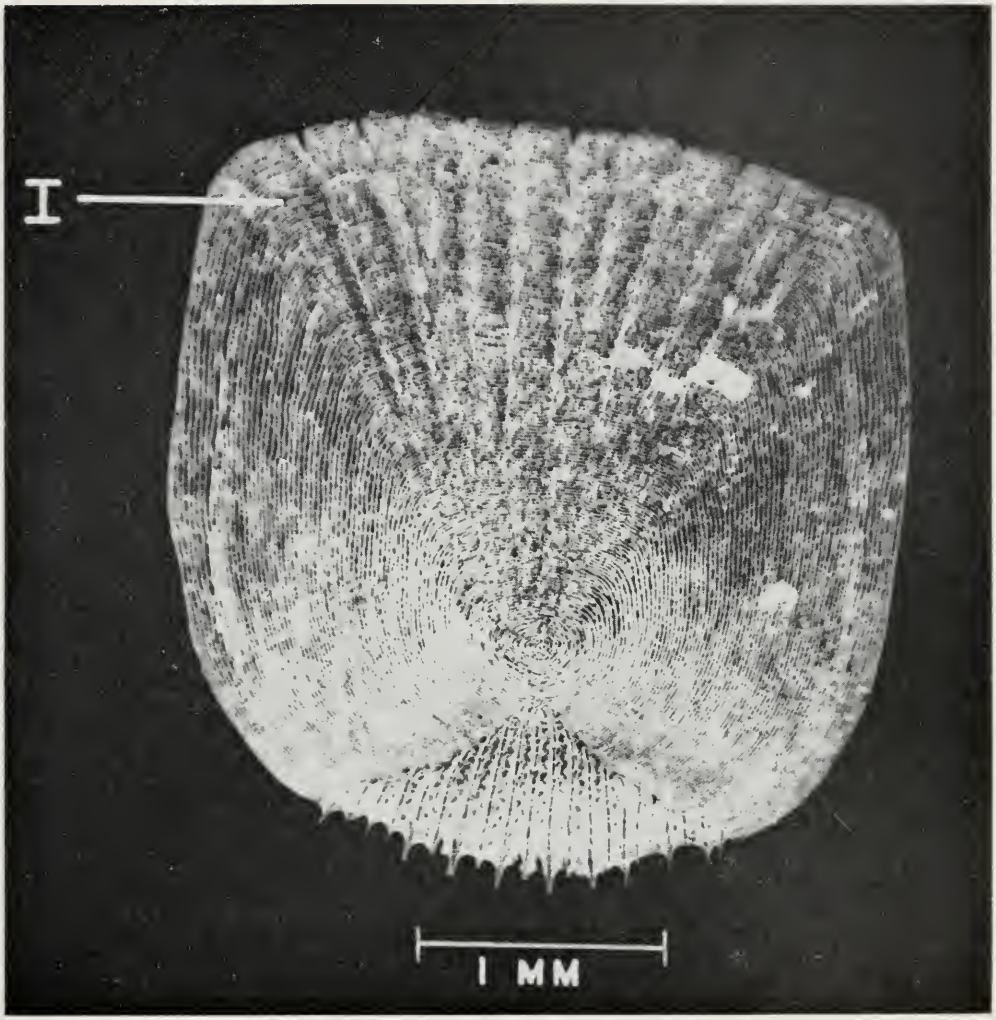



Figure 2. Scale of spot with one annulus (total length 140 mm, March 27, 1954).

drying. However, otoliths of spot preserved in formalin for more than a week were opaque and unusable.

Dakin (1939) and Arora (1951) ground otoliths to show the rings clearly. A few spot otoliths ground on a rotary abrasive wheel were compared with their entire counterparts and no significant difference was noticed in clarity of the rings.

The otoliths were placed in a black bakelite dish filled with water to a depth of about 4 mm and studied under a stereoscopic binocular microscope using reflected light. The translucent bands appeared opaque by reflected light in contrast to opaque zones which appeared white. The radius of the otolith from the center of the nucleus to the anterior edge and to the various annuli was measured by means of an eyepiece micrometer.

## Age and Growth

### *Results of Scale Studies*

*Description of the spot scale.*—Pacheco (1957) gave a brief description of the spot ctenoid scale. Taylor (1916) stated that the radii in *Cynoscion regalis* may afford a supplementary aid in locating annuli, for new radii often originate at an annulus. Pacheco (1957) also subscribed to the same view. Examination of the spot scale revealed that new radii originated at an an-

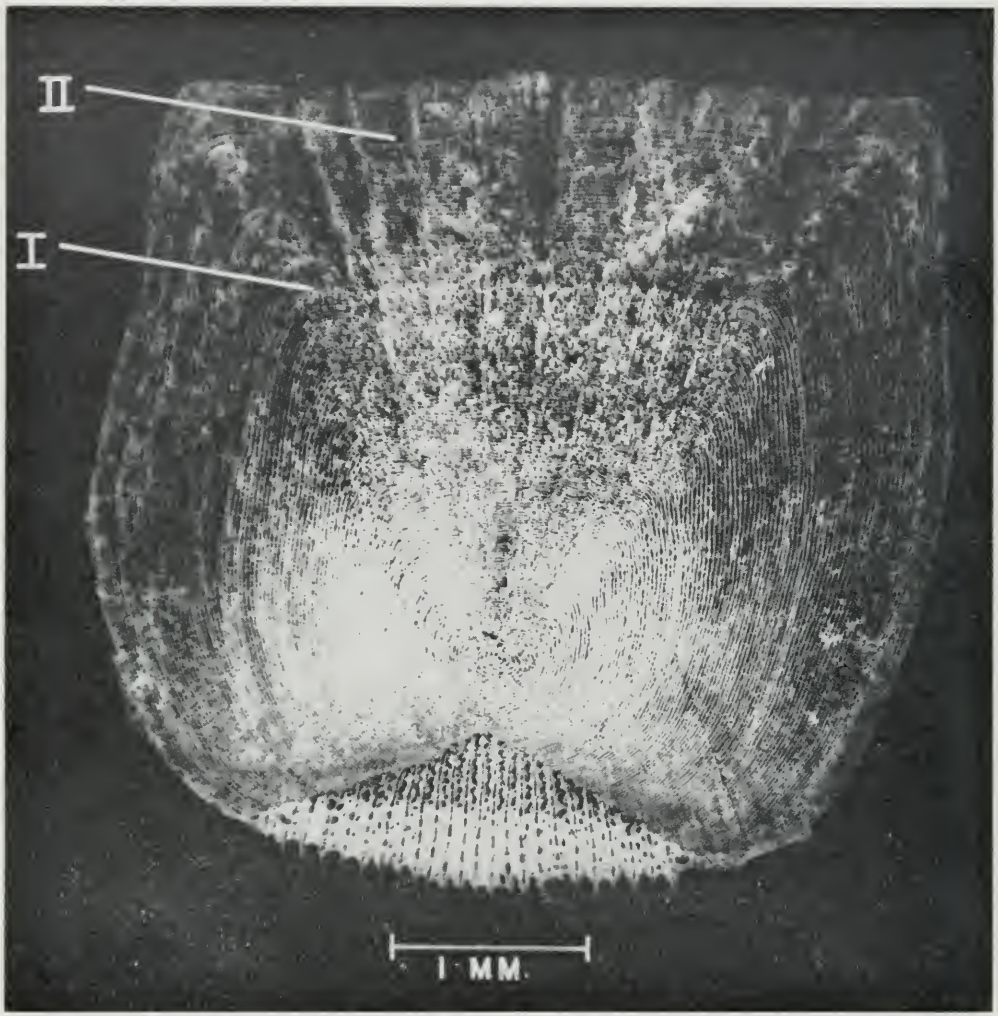



Figure 3. Scale of spot with two annuli (total length 220 mm, March 31, 1955).

nulus (fig. 4), although several exceptions were noted. However, with caution, radii may be used as an additional guide to locate an annulus. New radii usually arise in the antero-lateral field on the outside of the already existing radii. The posterior field of the scale is devoid of circuli and radii (figs. 2-4).

*Growth cessation marks.*—The characteristics of the spot annulus were determined after examination of about two hundred spot scales. The best character is "crossing over". This is especially evident at the lateral areas of the scale. The circuli in the anterior region of the annulus are broken, incomplete, crooked, or wavy, and stand out prominently from the circuli that precede and succeed them. The annulus is parallel to the general contour of the scale and can be traced around the sculptured part of the scale. Sometimes it can be traced on the unsculptured part of the scale (*i.e.*, in the region of the ctenii). The spot annulus has three characteristics by means of which it can be identified. The so-called crossing over at the lateral areas, the broken or interrupted circuli in the anterior field of the scale, and, at times, closely approximated circuli in the anterior field (figs. 2-4). A check was considered an annulus only when it was present in all scales of the selected sample. My observations agree with Pacheco

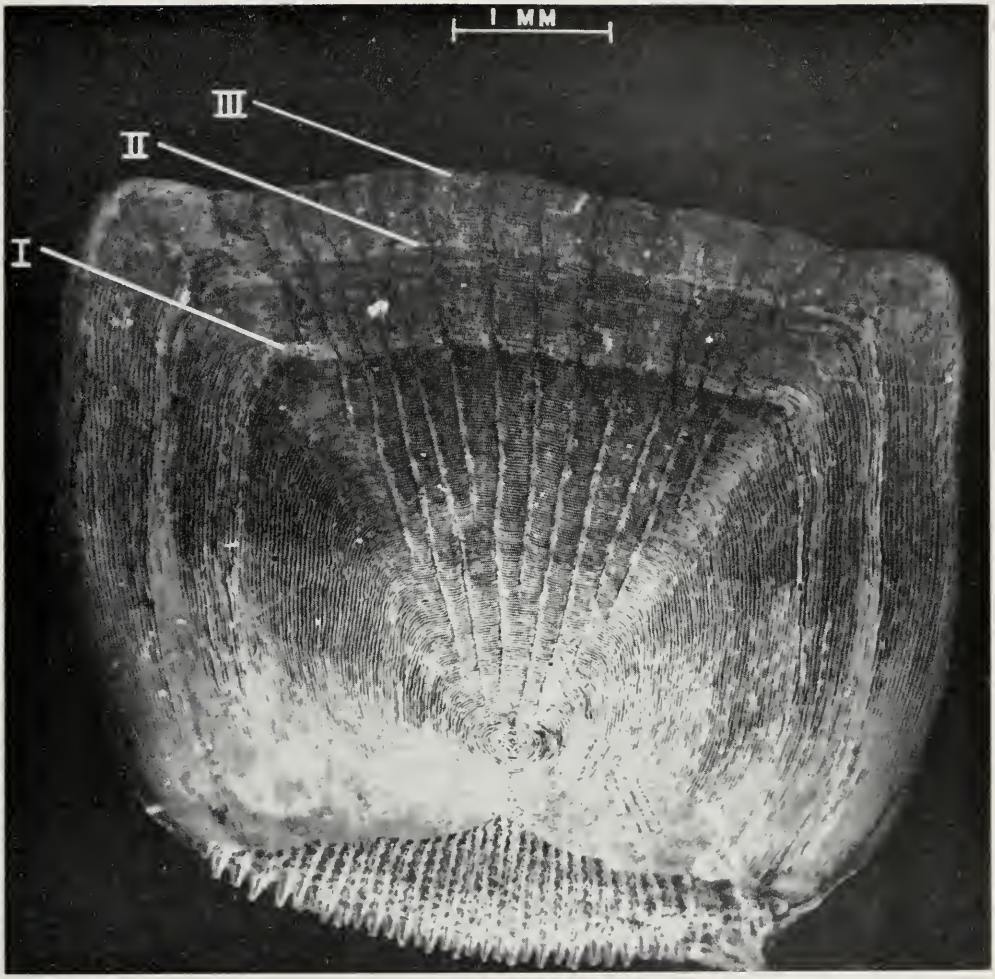



Figure 4. Scale of spot with three annuli (total length 243 mm, May 28, 1954).

(1957) who stated that the usual characteristic of a spot annulus was closer spacing of circuli associated with broken circuli most evident in the postero-lateral area of the scale.

False annuli were often encountered and with some practice they were easily identified. The false annulus is often close to an annulus and is more distinct in the anterior part of the scale than in the lateral areas. Sometimes it is more pronounced than an annulus. Its course cannot be followed all the way around the scale because the false annulus usually merges with the annulus. False annuli may be caused by spawning and/or by some adverse environmental condition.

*Period of annulus formation.*—Time of annulus formation was determined by measuring the marginal increments for all scales collected between October 1958 and September 1959. The mean marginal increment was minimum in March, and was maximum in January (fig. 5), and indicates that the annulus is formed in February and early March. After March the marginal increments increase very rapidly.

To verify the abovementioned determination all scales collected in January, February, and March of 1959 were re-examined. No annulus was noticed in scales collected in January 1959. An annulus was present in the majority of the scales collected in the latter part of February. The majority of the

Table 1.

*Mean lengths of the anterior scale radius (X 57.5), mean total length, mean number of circuli, and mean otolith radius of 1,418 spot.*

| Class Range | Number of Specimens | Mean Anterior Scale Radius | Mean Total Length | Mean Number of Circuli | Mean Otolith Radius in mm |
|---|---|---|---|---|---|
| (Total length in mm) | | | | | |
| 20- 29 | 7 | 9.6 | 26.7 | 7.6 | — |
| 30- 39 | 9 | 12.8 | 33.1 | 10.1 | — |
| 40- 49 | 7 | 22.4 | 43.1 | 23.6 | 1.22 |
| 50- 59 | 20 | 35.6 | 55.5 | 40.6 | 1.29 |
| 60- 69 | 41 | 44.9 | 65.3 | 48.4 | 1.42 |
| 70- 79 | 78 | 55.5 | 74.3 | 65.6 | 1.56 |
| 80- 89 | 90 | 65.3 | 84.2 | 73.6 | 1.71 |
| 90- 99 | 108 | 78.4 | 94.8 | 87.4 | 1.85 |
| 100-109 | 182 | 87.2 | 104.6 | 98.0 | 1.94 |
| 110-119 | 220 | 98.7 | 114.2 | 108.5 | 2.04 |
| 120-129 | 152 | 106.4 | 124.1 | 114.0 | 2.16 |
| 130-139 | 97 | 116.8 | 133.5 | 124.0 | 2.24 |
| 140-149 | 56 | 125.7 | 144.5 | 131.4 | 2.30 |
| 150-159 | 42 | 138.4 | 154.0 | 138.8 | 2.50 |
| 160-169 | 46 | 144.8 | 164.5 | 150.0 | 2.59 |
| 170-179 | 45 | 152.3 | 175.0 | 154.2 | 2.72 |
| 180-189 | 45 | 167.0 | 184.0 | 163.5 | 2.85 |
| 190-199 | 29 | 178.0 | 194.7 | 170.0 | 2.95 |
| 200-209 | 29 | 183.5 | 203.2 | 180.0 | 3.04 |
| 210-219 | 37 | 190.6 | 214.4 | 184.0 | 3.24 |
| 220-229 | 37 | 200.2 | 223.5 | 195.5 | 3.38 |
| 230-239 | 21 | 210.1 | 234.5 | 200.2 | 3.46 |
| 240-249 | 14 | 222.5 | 243.5 | 206.3 | 3.63 |
| 250-259 | 5 | 226.0 | 252.0 | 213.0 | 3.67 |
| 260-269 | — | — | — | — | — |
| 270-279 | 1 | 233.0 | 270.0 | 236.0 | 3.74 |

scales from March samples showed an annulus plus a small marginal increment; the remainder had an annulus but no marginal increment. Pacheco (1957) stated that annuli of spot in Chesapeake Bay are formed in October and November. The disparity in the time of annulus formation is possibly due to differences in latitude. The temperature does not drop appreciably in the Lake Pontchartrain area until November and December (Suttkus, Darnell, and Darnell, 1954).

*Age groups.*—The young usually first appear in Lake Pontchartrain in January. Pre-

Table 2.

*Average calculated total lengths and increments in length of spot collected from July 1953 to May 1954, January 1955 to September 1955, and October 1958 to September 1959, using scales.*

| Age Group | Number of Specimens | Average Length at Capture in mm | Average Calculated Lengths (in mm) for Previous Years of Life | | |
|---|---|---|---|---|---|
| | | | 1 | 2 | 3 |
| 0 | 1081 | 110.0 ( 21-197) | — | — | — |
| I | 269 | 163.1 (101-223) | 139.1 ( 90.7-185.8) | — | — |
| II | 90 | 218.7 (180-247) | 151.8 ( 87.2-191.6) | 200.5 (156.8-227.9) | — |
| III | 38 | 234.5 (210-270) | 150.9 (105.7-202.9) | 199.1 (168.0-224.0) | 223.2 (200.0-248.6) |
| Number of Records | 1418 | — | 337 | 128 | 38 |
| Average Calculated Lengths in mm | | | 143.8 | 200.1 | 223.2 |
| Average Increments in mm [2] | | | 143.8 | 48.7 | 24.1 |
| Average Total Length in Inches | | | 5.7 | 7.9 | 8.8 |

[2] Only fish completing year of life were used in computing increments.

sumably the eggs were spawned either in December or early January. Thus the biological year and the calendar year appear to coincide closely. The 1958 year class was spawned in late 1957 or early 1958 and formed the first annulus in February-March 1959. Thus a spot in the forementioned group was considered to be young-of-the-year during 1958 and of age group 0 until annulus formation in 1959. Photographs of scales from spot of different ages are presented in Figures 2-4. After all scales were "read" and interpreted the average total length for each age group was determined. The increase in length is greatest during the first year and thereafter the growth rate is a decreasing progression (Table 2).

*Determination of the length of the fish at the time of scale formation.*—Young fish (17 to 38 mm in total length) collected in February 1954 were used to determine the length of the spot at the time of scale formation. The skin was stripped off from head to tail and adherent muscle tissue was removed. It was streched on a slide and a drop or two of alizarin red was placed on it. After one minute the preparation was drained and the excess stain removed by washing in 70 percent alcohol. The skin was then dehydrated and mounted in Canada balsam.

Scales or scale papillae were not noticed in fish which were 17 mm, 19 mm, and 20 mm in total length. One specimen, 21 mm long (out of three) had scales or scale papillae. Two circuli were observed on caudal peduncle scales from four fish that were 22 mm in total length. Twenty-two millimeters total length was considered to be the length of the fish at the time of scale formation. This value was used in back-calculation of body lengths.

There is a row of scales along the lateral line from the caudal fin to the edge of the operculum of fish 24 mm in total length. A group of scales extends ventrally from the middle of the lateral line system. Scales are absent on either side of the mid-dorsal and mid-ventral line.

Scales are present on either side of the mid-ventral line in 26 mm fish but the scales are not imbricate.

All scales are fully developed and imbricate in 31 mm fish.

Hildebrand and Cable (1930) working at Beaufort, North Carolina, reported that the scales were not visible on spot 25 mm

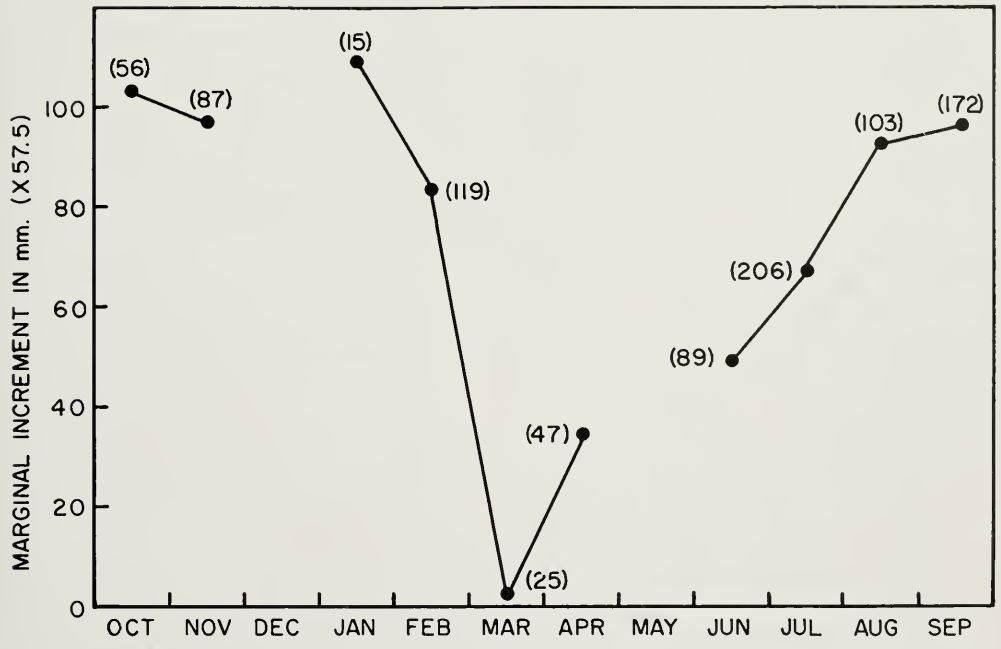



Figure 5. Mean monthly marginal increments of the scale of spot. Figures in parentheses indicate number of specimens.

long but were evident nearly everywhere on fish 30 mm long.

*Body length and scale length relationship.*—According to Creaser (1926), Graham (1928), Van Oosten (1929), Hile (1941), and Lagler (1956) scales remain constant in number and retain their identity throughout the life of a fish. Johnston (1905) was the first to devise a method of calculating the length of a fish for each year of its life by comparing the widths of the yearly areas of the scale.

The relationship of total length to scale length was determined from measurements of 1,418 spot. The individual measurements of both the total length and the anterior scale radius for each of the 1,418 spot were plotted on millimeter graph paper and a linear distribution was found. The data were grouped by total lengths into 10 mm groups (Table 1, fig. 6). The averages of these groups and the means of their respective scale radii (X 57.5) were then used in computing the linear regression equation (Snedecor, 1957): $Y = 0.98693X + (-18.333)$, where Y = anterior scale radius in millimeters (X 57.5), and X = total length in millimeters.

*Estimates of annual growth.*—Creaser (1926), Rounsefell and Everhart (1953), and Lagler (1956) list several formulae for back-calculation of body lengths. One frequently used formula is the modified form of Fraser (1916):

$$L' = C.F. + \frac{S'}{S}(L - C.F.).$$

The length of fish at the end of each year of life was computed for all fish with at least one annulus using Fraser's formula. The results are shown in Table 2 and the calculated growth curve based on these data is shown in Figure 7.

The greatest annual increment (143.8 mm) was during the first year of life

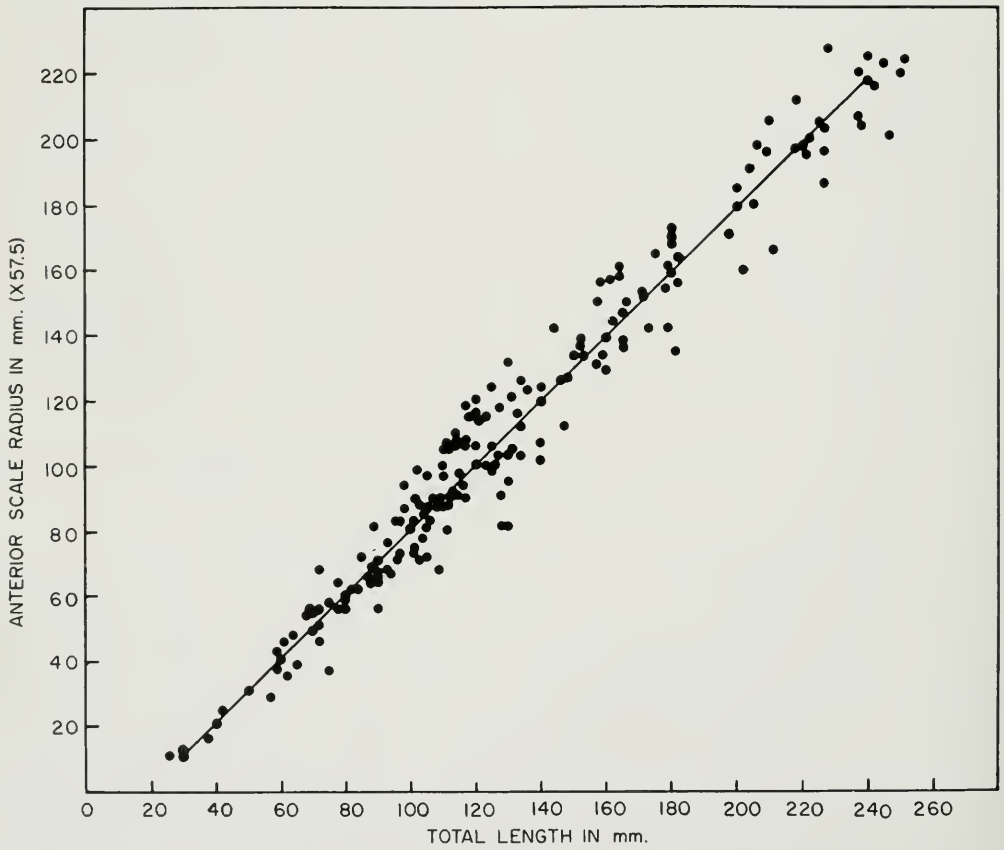



Figure 6. Relationship between total length and anterior scale radius for 1,418 spot. Only 200 random statistics plotted. Line plotted for $Y = 0.98693X + (-18.333)$.

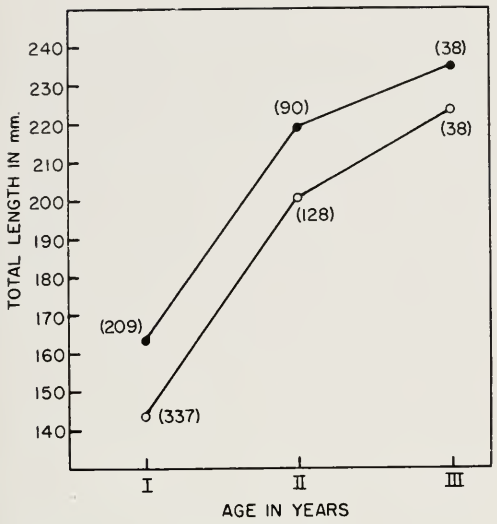



Figure 7. Growth curves of the spot. Dots=observed growth; circles=calculated growth. Figures in parentheses indicate the number of specimens.

(Table 2). During the second and third years of life the increments were 48.6 mm and 24.1 mm respectively.

Calculated lengths are higher than ob-observed lengths of fish collected during the year of growth (Table 2, fig. 7). For instance, the age group 0 consisted mostly of small fish (24 to 197 mm) (Table 2). The calculated length at the end of the first year is higher than the observed length during the year.

Specimens collected in three different years were compared to ascertain differences, if any, in rates of growth. Tables 3, 4, and 5 show the calculated total lengths and increments during the years 1953-54, 1955, and 1958-59 respectively. Average calculated lengths for various age groups during the year 1953-54 agree very closely with the values in Table 2. But, during the year 1955 the calculated lengths at the end of the first year are higher than those during 1953-54. This shows that in 1955 the fish attained larger lengths at the end of the first year of life. Growth was slow during the first year of the one plus individuals for 1958-59 sample (Table 5). The length attained at the end of the first year during 1958-59 was 123.1 mm compared to 145.9 mm during 1953-54 and 156.4 mm during 1955. Further study will be necessary to determine the nature of factors responsible for the disparity in length increments. A comparison of growth rates between Rigolets and Lake Pontchartrain spot is not advisable because the samples were taken in different years.

An analysis of the age and growth of 119 spot collected on October 17 and 22, 1953 is shown in Table 6. These results agree closely with 1953-54 set, and thus substantiate the validity of the use of samples obtained over an extended period of time.

The growth of the various year classes in different calendar years is presented in Table 7. The average annual increments demonstrate that the amount of growth made by fish in a particular year of life varied from year to year. Various factors are probably responsible for these fluctuations in annual growth.

TABLE 3.
*Average calculated total lengths and increments in length of spot collected from July 1953 to May 1954, using scales.*

| Age Group | Number of Specimens | Average Calculated Length (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 90 | 142.1 | — | — |
| II | 65 | 149.1 | 197.5 | — |
| III | 32 | 150.4 | 197.5 | 222.5 |
| Number of Records | 187 | 187 | 97 | 32 |
| Average Calculated Lengths in mm | | 145.9 | 197.5 | 222.5 |
| Average Increments in mm [3] | | 145.9 | 47.9 | 25.0 |

[3] Only fish completing year of life were used in computing increments.

TABLE 4.
*Average calculated total lengths and increments in length of spot collected from January 1955 to September 1955, using scales.*

| Age Group | Number of Specimens | Average Calculated Length (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 52 | 155.6 | — | — |
| II | 23 | 158.9 | 207.3 | — |
| III | 6 | 153.9 | 207.7 | 226.7 |
| Number of Records | 81 | 81 | 29 | 6 |
| Average Calculated Lengths in mm | | 156.4 | 207.3 | 226.7 |
| Average Increments in mm [4] | | 156.4 | 49.5 | 19.4 |

[4] Only fish completing year of life were used in computing increments.

The average total lengths of young-of-the-year spot collected at almost the same time, at the same locality (Point Aux Herbes, south shore of Lake Pontchartrain) and in different years were compared to ascertain differences in the time of spawning. For example, 1954 year class collected on March 7, 1954 at Point Aux Herbes had attained a mean total length of 35.2 mm, with a range from 20-50 mm. The 1958 year class collected on March 14, 1958 at the same locality had attained a mean total length of 24.8 mm, with a range from 20-32 mm. This would indicate that the 1958 year class was spawned later than the 1954 year class. Further, the 1954 and 1958 year classes attained increments of 155.7 mm and 122.1 mm respectively during the first year of life (Table 7). This disparity in the increments appears to be the result of late spawning of the 1958 year class.

Pearson (1928) found a negligible number of spot over 182 mm in length. Using the age-length ratio of Welsh and Breder (1923) he advanced a hypothesis that spot died before their third year. Gunter (1945) working in Texas waters also corroborated Pearson's hypothesis. Very few spot with three annuli were collected from Louisiana waters and I also assume that the majority of the spot die before they attain three years of age. Welsh and Breder (1923) reported a spot 300 mm in total length which they determined to be 4½ years old. According to them the maximum length recorded for this species is 330 mm. The longest specimen used in this study was 270 mm in total length and the scales had three annuli plus a marginal increment.

TABLE 5.
*Average calculated total lengths and increments in length of spot collected from October 1958, to September 1959, using scales.*

| Age Group | Number of Specimens | Average Calculated Length (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 67 | 122.1 | — | — |
| II | 2 | 157.0 | 215.9 | — |
| III | — | — | — | — |
| Number of Records | 69 | 69 | 2 | — |
| Average Calculated Lengths in mm | | 123.1 | 215.9 | — |
| Average Increments in mm [5] | | 123.1 | 58.9 | — |

[5] Only fish completing year of life were used in computing increments.

TABLE 6.
*Average calculated total lengths and increments in length of spot collected on October 17 and 22, 1953, using scales.*

| Age Group | Number of Specimens | Average Calculated Length (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 9 | 143.8 | — | — |
| II | 31 | 153.5 | 198.2 | — |
| III | 9 | 138.4 | 191.0 | 218.0 |
| Number of Records | 49 | 49 | 40 | 9 |
| Average Calculated Lengths in mm | | 148.9 | 196.5 | 218.0 |
| Average Increments in mm [6] | | 148.9 | 46.4 | 27.0 |

[6] Only fish completing year of life were used in computing increments.

Welsh and Breder (1923) found that spot in New Jersey are approximately 80 to 100 mm in total length when one year old, 170 to 220 mm when two years old, 240 to 290 mm when three years old.

Townsend (1956) working on the age and growth of spot in Alligator Harbor, Florida, examined scales from 13 spot of various sizes. Four of them had one annulus each, three had two, one had three, and the rest (five) had no annuli. He did not test the validity of these age marks.

Pacheco (1957) studied scales of Chesapeake Bay spot and found the mean total length attained at the end of first year was about 196 mm, and 247.9 mm at the end of the second year.

The figures of Pacheco (1957) are higher than those of Welsh and Breder (1923) and greater than those obtained in the present study, *i.e.*, the total length attained at the end of the first year is 143.8 mm, 200.1 mm at the end of the second year, and 223.2 mm at the end of the third year. Thus the average size at each age and rate of growth appear to vary greatly throughout the range of this species.

*Circuli.*—The number of circuli was enumerated from focus to each annulus and to the anterior margin of the scale (Table 8). The increase in the number of circuli is greatest during the first year and thereafter, the number of circuli formed is less. There is a linear relationship between total length and the number of circuli (fig. 8) thus in-

dicating that the circuli are more or less evenly spaced. In age group 1, the average number of circuli is 147.6; of this number 128.9 were formed before the formation of the first annulus and 18.5 were formed after it. On the average, 132.1 circuli are laid down from focus to first annulus and 38.3 circuli are laid down from first annulus to second annulus, and second annulus and third between second and third annuli (Table 8). There is good agreement regarding the average number of circuli laid down between focus and first annulus, first annulus and second annulus and about 20.1 are laid down annulus in the different age groups. The range of variation of the number of circuli appears to be considerable (Table 8), but some of this variation is a reflection of range of lengths of the fish. Nevertheless, the number of circuli may be used to determine the approximate age of spot in fractions of a year.

*Results of Otolith Studies*

*Description of the spot otolith.*—The otolith is oval, laterally compressed with a convex and a concave surface. The anterior end is bluntish while the posterior end is rounded. When *in situ* the concave surface faces toward the outside in the otic capsule. Each otolith has a central translucent area known as the nucleus. The nucleus is surrounded by alternating bands of wide opaque and narrow translucent bands (figs. 10-12). Usually several radiating bands proceed from the center toward the margin of the nucleus (figs. 10-12) but these bands seldom extend beyond the nucleus. The annuli are clearly seen on the concave side of the otolith. On the convex side a deep groove extends from the center of the otolith towards the anterolateral part.

The otolith of a young spot differs slightly from that of an adult spot. It is oval with the central nucleus surrounded by a wide opaque area. The anterior end is blunt and the posterior end is rounded. In young specimens most otoliths have a translucent ring. Eventually, the translucent ring is not continuous and seldom goes all the way around the nucleus (fig. 9). As spot gets larger radiating translucent lines proceed from the nucleus toward the translucent ring around the nucleus but this ring is joined to the nucleus by means of radiating

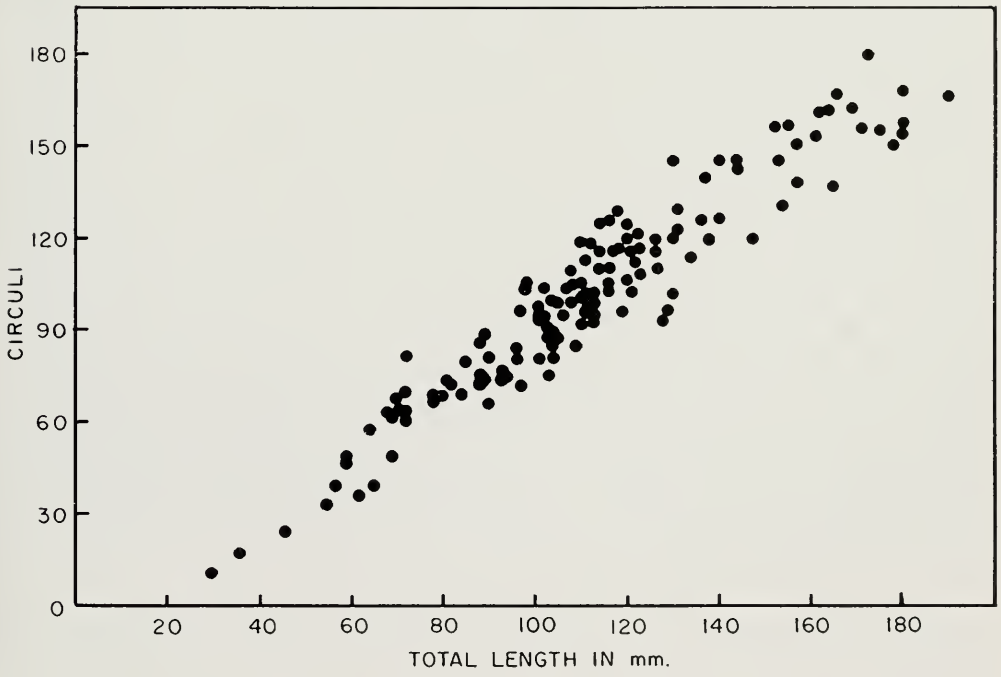



Figure 8. Relationship between total length and the number of circuli for age group 0. Only 145 random statistics plotted.

TABLE 7.

*Annual growth increments (in millimeters) of spot in 1950-54, 1957, and 1958 year classes during the calendar years 1950-54, and 1956-58, using scales. Figures in parentheses indicate year of life.*

| Year Class | Year Collected | Increments of Growth in Calendar Years | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1950 | 1951 | 1952 | 1953 | 1954 | 1955 | 1956 | 1957 | 1958 |
| 1950 | 1953 | 146.7 (1) | 49.9 (2) | 26.0 (3) | — | — | — | — | — | — |
| 1951 | 1953 | — | 155.6 (1) | 43.2 (2) | — | — | — | — | — | — |
| 1951 | 1954 | — | 163.7 (1) | 43.8 (2) | 14.7 (3) | — | — | — | — | — |
| 1952 | 1953 | — | — | 146.3 (1) | — | — | — | — | — | — |
| 1952 | 1954 | — | — | 148.5 (1) | 42.7 (2) | — | — | — | — | — |
| 1952 | 1955 | — | — | 153.9 (1) | 53.7 (2) | 19.2 (3) | — | — | — | — |
| 1953 | 1954 | — | — | — | 143.6 (1) | — | — | — | — | — |
| 1953 | 1955 | — | — | — | 158.8 (1) | 52.8 (2) | — | — | — | — |
| 1954 | 1955 | — | — | — | — | 155.7 (1) | — | — | — | — |
| 1956 | 1958 | — | — | — | — | — | — | 157.3 (1) | 58.6 (2) | — |
| 1958 | 1959 | — | — | — | — | — | — | — | — | 122.6 (1) |
| Number of Fish in Each Year Class | | 25 | 58 | 44 | 89 | 52 | — | 2 | — | 67 |

lines. Before the formation of the first annulus the nucleus merges with the translucent ring. Arora (1951) also described radial lines that run from the core to the periphery in the otoliths of *Citharichthys sordidus*.

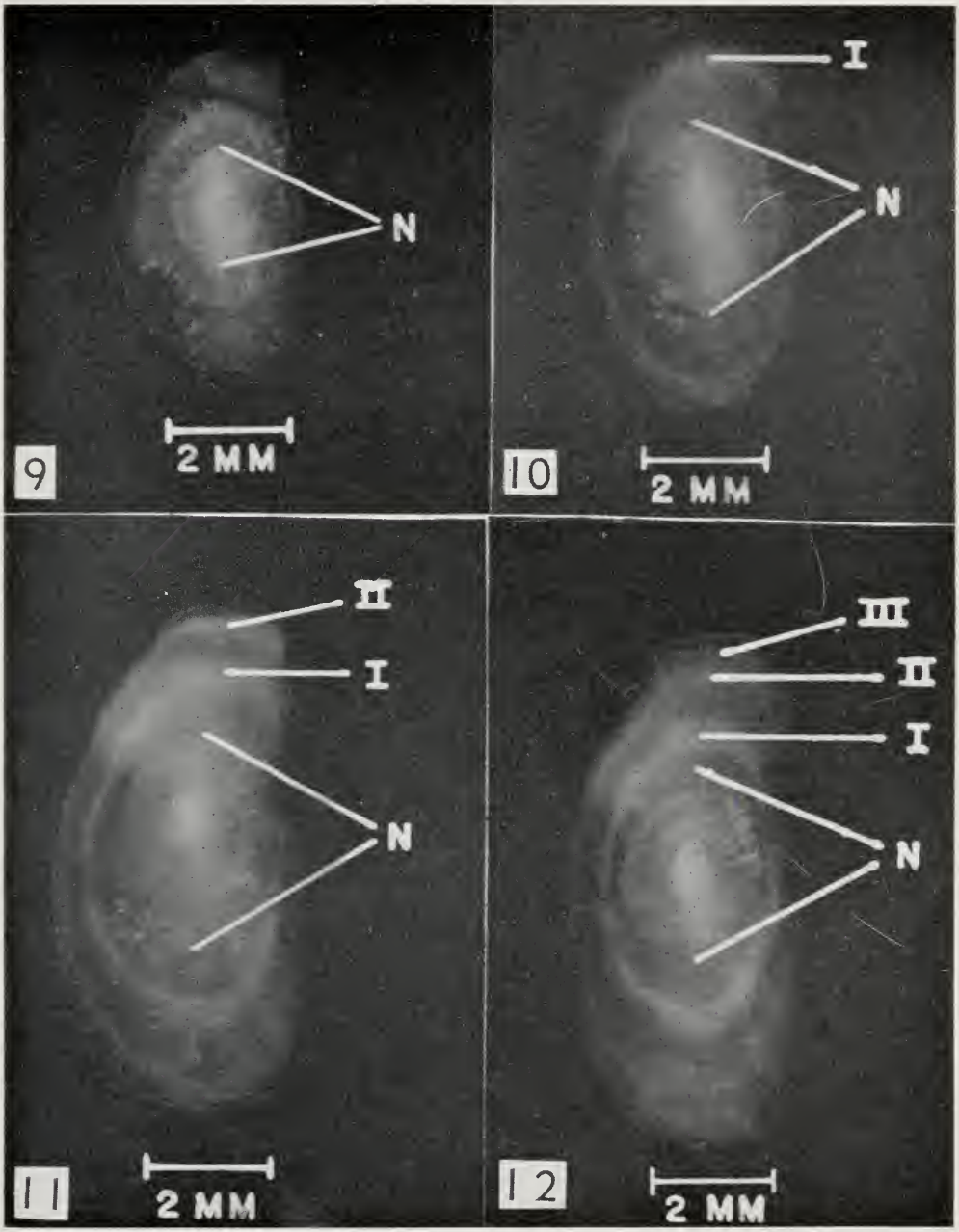
*Growth cessation marks.*—Cunningham (1905), Hickling (1931, 1933), Molander (1947), and Arora (1951) stated that the opaque bands are due to increased calcification which occurs during summer, the period of rapid growth, and that the translucent bands are formed during winter when growth is slow.

Walford and Mosher (1943) used the following criteria to distinguish annuli in Pacific sardine otoliths. According to them "An annulus is a more or less translucent band concentric with the margin of the otolith, the intervening spaces being opaque. It can usually be traced entirely around the otolith, although it is more easily observed

TABLE 8.

*Relationship between number of circuli and age of spot collected from July 1953 to May 1954, January 1955 to September 1955, and October 1958 to September 1959.*

| Age Group | Average Length at Capture in mm | Average No. of Circuli | Number of Specimens | Average No. of Circuli from Focus to First Annulus | Average No. of Circuli from First Annulus to Second | Average No. of Circuli from Second Annulus to Third |
|---|---|---|---|---|---|---|
| 0 | 110.0 | 98.8 ( 4-174) | 1081 | — | — | — |
| I | 163.1 | 147.6 ( 96-199) | 209 | 128.9 ( 89-175) | — | — |
| II | 218.7 | 190.0 (145-222) | 90 | 135.3 ( 85-182) | 39.4 (18-75) | — |
| III | 234.5 | 207.1 (175-236) | 38 | 142.2 (110-181) | 35.8 (19-64) | 20.1 (11-33) |
| Number of Records | — | — | 1418 | 337 | 128 | 38 |
| Average Number of Circuli | | | | 132.1 | 38.3 | 20.1 |




Figures 9-12. Otoliths of spot; N = nucleus. **9.** Without annulus; note the false translucent ring around nucleus (total length 141 mm, October 23, 1958). **10.** With one translucent annulus (total length 180 mm, May 5, 1955). **11.** With two translucent annuli (total length 237 mm, May 5, 1955). **12.** With three translucent annuli (total length 250 mm, May 5, 1955).

TABLE 9.

*Average calculated total lengths and increments in length of spot collected from January 1955 to September 1955 and October 1958 to September 1959, using otoliths.*

| Age Group | Number of Specimens | Average Calculated Lengths (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 123 | 149.2 (109.0-200.0) | — | — |
| II | 21 | 176.3 (137.2-198.9) | 214.7 (199.0-238.0) | — |
| III | 6 | 158.6 (137.0-183.0) | 204.5 (180.0-239.0) | 225.1 (197.4-260.1) |
| Number of Records | 150 | 150 | 27 | 6 |
| Average Calculated Lengths in mm | | 153.3 | 212.0 | 225.1 |
| Average Increments in mm [7] | | 153.3 | 40.0 | 20.6 |
| Average Total Length in Inches | | 6.0 | 8.3 | 8.9 |

[7] Only fish completing year of life were used in computing increments.

at the blunter anterior end than at the sides or posterior end. Annuli tend to be zones rather than lines."

These criteria also apply to spot otoliths. The annuli, as in the Pacific sardine, are very prominent in the anterior blunt end (figs. 10-12).

False annuli were noticed occasionally. They were in the form of translucent bands, but they were always incomplete and hence were easily recognized.

*Determination of the period of annulus formation.* — The incidence of translucent margins was plotted as a percentage of all otoliths examined during each month of the year (Fairbridge, 1951; Ling; 1958). One thousand and sixty-four spot otoliths collected during the periods January 1955 to September 1955, and October 1958 to September 1959 were used. The otoliths were read without knowledge of the date of collection and were classified as having a translucent or an opaque margin (fig. 13). Annulus formation began in January and con-

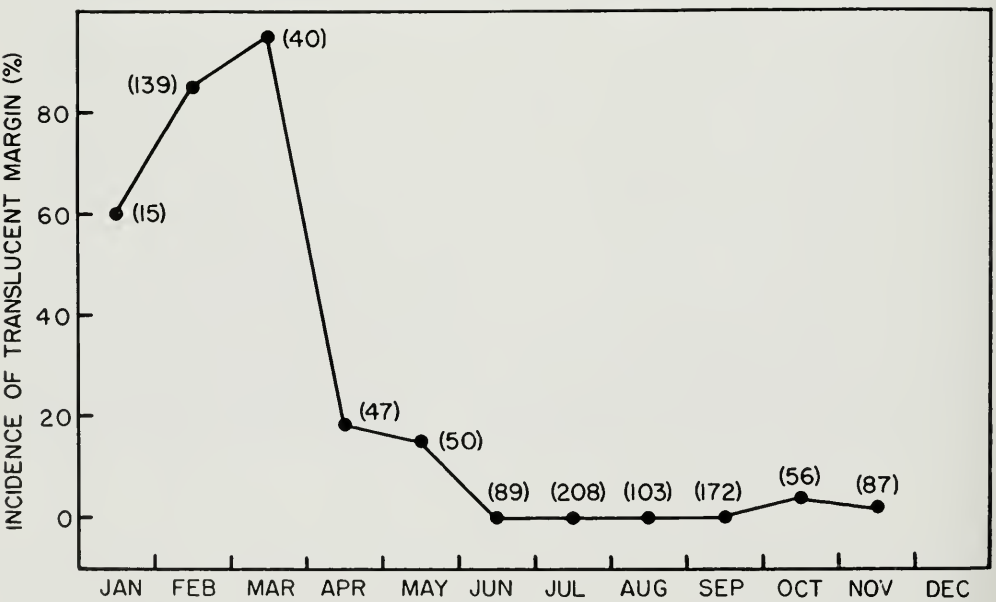



Figure 13. Monthly percentage incidence of translucent otolith margins. Figures in parentheses indicate the number of specimens.

tinued through February and March. During February 85 percent of the otoliths already had the annulus. These data correspond with the period of annulus formation determined by scale examination.

*Age groups.*—The writer assumed that the nucleus surrounded by the opaque zone covered the period of life from the time of hatching until the formation of the first annulus. The nucleus represents the initial deposition of calcareous material and is comparable to the focus of the scale. Hickling (1933), Moore (1947), and Ling (1958) have, however, counted the nucleus also. All workers agree that the translucent band is formed during winter and the opaque band during summer.

Hickling (1933) and Ling (1958) counted the opaque zones in hake otoliths and in sea garfish otoliths respectively and assigned the age according to the number of these bands. In the sea garfish (Ling, 1958) an annulus is laid down around an opaque nucleus after about the first six months of life and the first opaque band is formed at the end of the first year. Hence he counted the opaque zones and assigned the fish to year groups according to the number of these bands. The spot otolith is a little different. The opaque zone surrounding the nucleus represents the growth during the spring, summer, and fall. The annulus is formed around the opaque zone some time in February. The presence of a translucent annulus indicates that the fish has passed through one winter and hence is a year old; ages were recorded in the number of winters completed. Thus a spot in its first year of life belongs to age group 0 and its otolith has no translucent annulus. A spot in its second year belongs to age group 1 and its otolith has one translucent annulus. Photographs of otoliths from spot of different ages are presented in Figures 9-12.

TABLE 10.
*Average calculated total lengths and increments in length of spot collected from January 1955 to September 1955, using otoliths.*

| Age Group | Number of Specimens | Average Calculated Length (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 61 | 165.2 | — | — |
| II | 19 | 176.6 | 214.6 | — |
| III | 6 | 158.6 | 204.5 | 225.1 |
| Number of Records | 86 | 86 | 25 | 6 |
| Average Calculated Lengths in mm | | 167.2 | 212.0 | 225.1 |
| Average Increments in mm [8] | | 167.2 | 39.8 | 20.6 |

[8] Only fish completing year of life were used in computing increments.

TABLE 11.
*Average calculated total lengths and increments in length of spot collected from October 1958 to September 1959, using otoliths.*

| Age Group | Number of Specimens | Average Calculated Length (in mm) for Previous Years of Life | | |
|---|---|---|---|---|
| | | 1 | 2 | 3 |
| I | 61 | 133.4 | — | — |
| II | 2 | 166.8 | 211.5 | — |
| III | — | — | — | — |
| Number of Records | 63 | 63 | 2 | — |
| Average Calculated Lengths in mm | | 134.4 | 211.5 | — |
| Average Increments in mm [9] | | 134.4 | 44.7 | — |

[9] Only fish completing year of life were used in computing increments.

*Body length and otolith radius relationship.*—Hickling (1933) in the hake, Fairbridge (1951) in tiger flathead, Grainger (1953) in Arctic char, Scott (1954) in yellowtail flounder, and Ling (1958) in sea garfish established a relationship between body length and otolith length.

The relationship of total length to otolith radius was determined from measurements of 1,064 spot. The individual measurements of both total length and otolith radius for each of the 1,064 spot were plotted on millimeter graph paper and a linear relationship was found. The data were grouped by total lengths into 10 mm groups (Table 1). The averages of these groups and the means of their respective otolith radii were used in computing the regression equation. Because the distribution was a straight line relationship, linear regression was followed (Snedecor, 1957). The following equation was derived: $Y = 0.16438X - 9.4418$, where Y = otolith radius in micrometer divisions, and X = total length in millimeters. Arbitrary values were substituted for X in the equation and the values for Y were obtained which were used to construct a regression line (fig. 14). Extrapolation of the line indicates a fish of no length has an otolith with a radius of almost 0.68 mm.

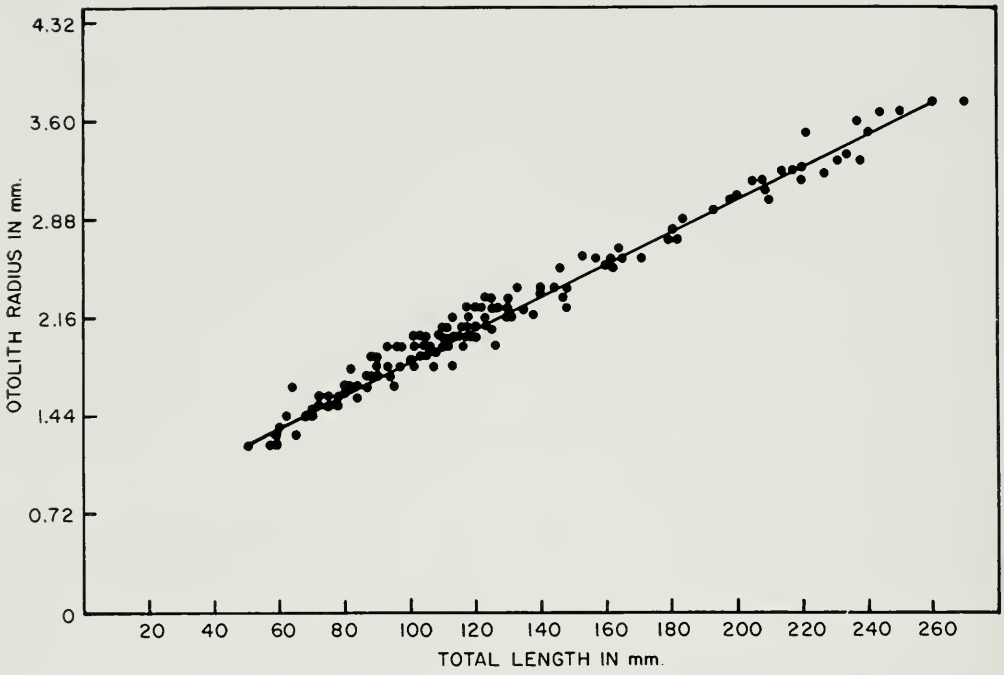



Figure 14. Relationship between total length and otolith radius for 1,064 spot. Only 120 random statistics plotted.

Ling (1958) reported a similar situation in sea garfish. There appears to be a nonlinear relationship between the radius of the spot otolith and the total length of the spot during the early larval period. After a certain period of growth the relationship is linear (fig. 14). No attempt was made to find the length of fish at the time of otolith formation.

*Estimates of annual growth.*—The calculation of intermediate lengths from otoliths has seldom been attempted. However, Hickling (1933) back-calculated the size of age group 0 hake. Fairbridge (1951) calculated intermediate lengths of New South Wales tiger flathead. Grainger (1953), Scott (1954), and Ling (1958), back-calculated the lengths at previous ages from measurements of otoliths of Arctic char, yellowtail flounder, and sea garfish respectively. All these authors assumed that the growth in fish length is proportional to growth in otolith length. Figure 14 indicates that in spot, growth in fish length is proportional to growth in otolith radius. The concentric bands in the otoliths have already been shown to be annual in formation The formula used for calculating the intermediate lengths was $l = \frac{L}{V} \times v$, where l = intermediate length; L = length of fish at capture; V = total otolith diameter; and, v = distance from center of the nucleus to the annulus. The length of the fish at the end of each year of life was computed for all fish with at least one annulus (Table 9).

The greatest increase in length (153.3 mm) took place during the first year of life. During the second and third years of life the increments were 40.0 mm and 20.6 mm respectively.

Table 9 represents a composite of 1955 and 1958-59 collections; separate tabulations were computed also (Tables 10 and 11 respectively). The increment for the 1955 sample during the first year was 167.2 mm, 39.8 mm during the second and 20.6 mm during the third year. A perusal of Table 11 indicates that the annual increment during the first year of life was very small when compared to that in 1955. Possibly this is correlated with the time of spawning, availability of food, temperature, etc. Obviously

growth patterns vary considerably in the same area from year to year and in adjoining areas because of the variations and fluctuations in ecological conditions.

### *Correlation of Scale and Otolith Readings*

Walford and Mosher (1943) advanced the method of age determination in Pacific sardines by correlating the age marks on both scales and otoliths. Moore (1947) correlated the age marks on scales and otoliths of sand flounder, while Arora (1951) did the same in the California sand dab.

Parallel age determination by scales and otoliths were made in 1,064 spot. Age determinations were made separately for the years 1955 and 1958-59 (figs. 15, 16). An inspection of the figures indicates that the calculated lengths based on scales and those based on otoliths are close and either may be used for age determination.

### *Length-frequency Distributions*

The total length measurements of the spot in Lake Pontchartrain taken by Suttkus, Darnell, and Darnell (1954) during 1953, 1954, and 1955 were classified into size groups with a class interval of 5 mm. The length-frequency distribution of each sample was prepared and the samples were combined by months (fig. 17).

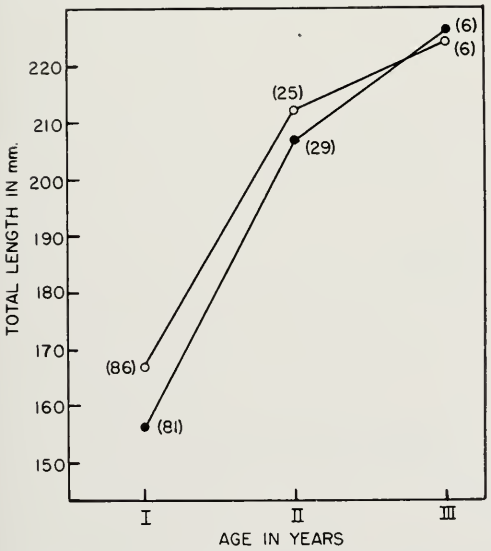



Figure 15. Growth curves of spot showing average calculated lengths from scale and otolith measurements. Dots = calculated lengths based on scales (1955); circles= calculated lengths based on otoliths (1955). Figures in parentheses indicate the number of specimens.

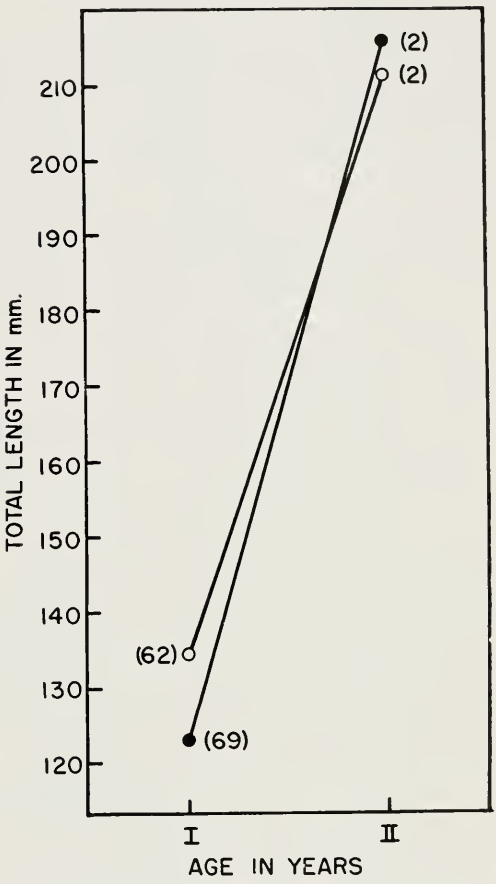



Figure 16. Growth curves of spot showing average calculated lengths from scales and otolith measurements. Dots = calculated lengths based on scales (1958-59); circles= calculated lengths based on otoliths (1958-59). Figures in parentheses indicate the number of specimens.

*Age group 0.*—Judging from Figure 17 a new group of fish appeared in January 1954 ranging in body length from 15 to 24 mm with a modal peak at 22 mm. The growth of this young-of-the-year group can be followed easily. In February 1954 the range was from 15 to 39 mm with a modal peak at 27 mm. By March 1954, they had attained a modal length of 37 mm with a range from 20 to 74 mm. The modal lengths during April, May, and June were 62, 67, and 92 mm respectively. But in July there are three "peaks", one at 107 mm, a second

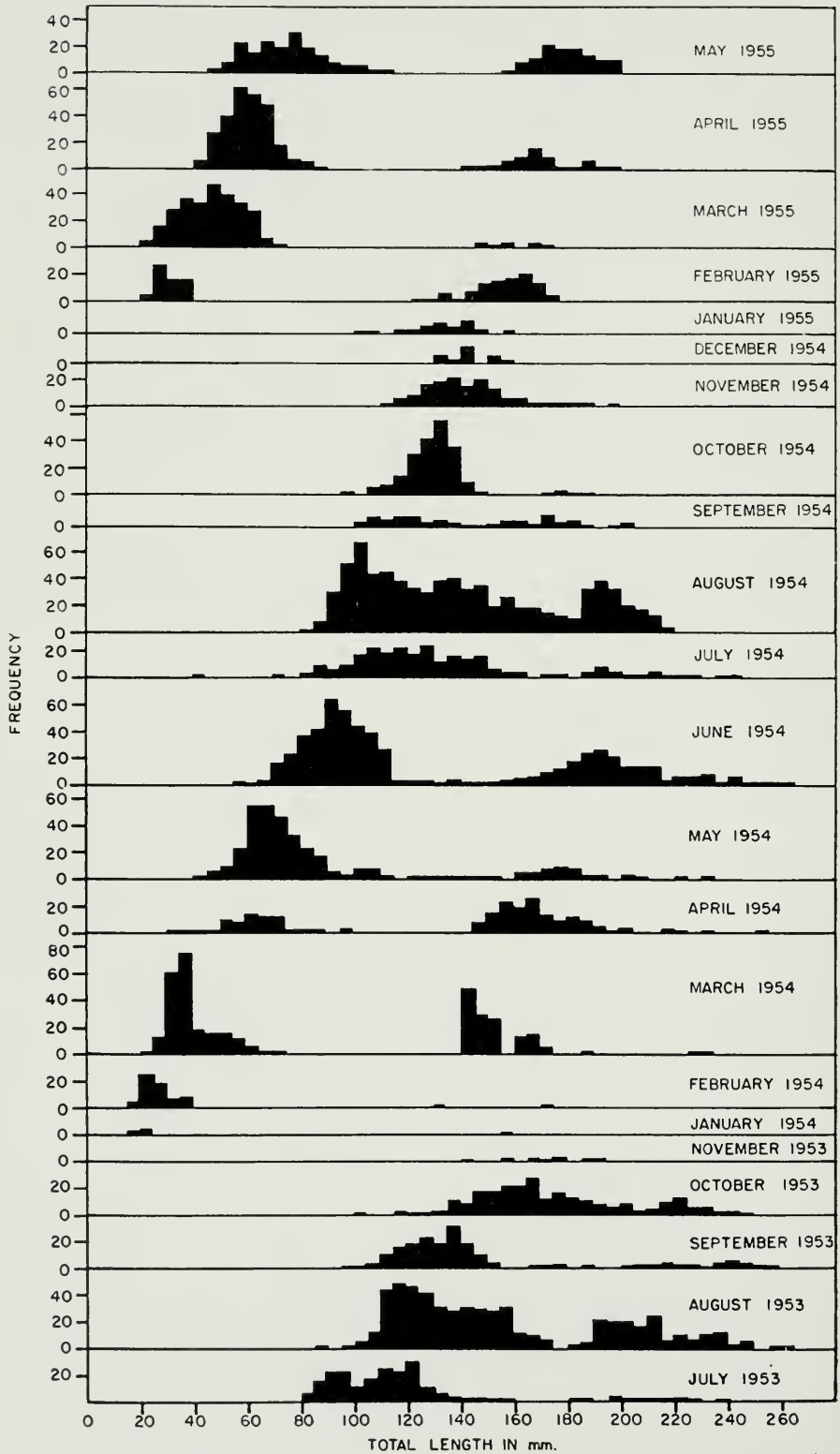



Figure 17. Length-frequency histograms of collections of spot made during 1953-54-55.

at 117 mm, and a third at 127 mm. As the length-frequency distribution is a consolidation of all samples taken at the various stations in Lake Pontchartrain, one might reasonably expect bimodal and trimodal distributions. These differences may be due to differences in nutrition. By December, the young-of-the-year had attained a modal length of 142 mm with a range from 130 to 150 mm. The distribution is bimodal in January with peaks at 132 mm and 142 mm. By the end of January 1955 the group that was spawned in winter of 1953-54 was approximately one year old (*i.e.,* they had passed through one winter). They attained a modal length of 142 mm. The calculated length at the end of first year by means of scales and otoliths is 143.8 mm and 153.3 mm respectively which is reasonable agreement.

A comparison of the monthly station samples of the young-of-the-year spot was made over a period of five months (April 1954 through August 1954). The results indicate that there was a difference in the mean total lengths for the spot taken from the various stations. For example, Bayou St. John spot (June—86.9 mm; August—98.4 mm) averaged smaller than those from South Draw (June—93.0 mm; August—120.3 mm) and Kenner Towers (June—92.5 mm; August—114.9 mm) although collected on or about the same date, with the same kind of gear. The young spot presumably group in the lake after their entry and remain in more or less separate populations throughout spring and summer. Suttkus (1955) reported a consistent difference between the mean lengths for young croakers *(Micropogon undulatus)* taken from various stations in Lake Pontchartrain. Bayou St. John croakers averaged considerably smaller than those from South Draw and Kenner Towers. Data were available for various stations in the lake, but the number of spot collected at these stations was not large enough to warrant a comparison. However, in Lake Pontchartrain, there appear to be great differences in rates of growth. Extrapolation of these results of one study area to another widely separated or adjoining is hazardous.

*Age group I.*—The growth of age group I can be continued beyond January 1955 by following the modes in February, March, April, and May 1955. Age group I had attained a modal length of 172 mm by May 1955 with a range from 155 to 199 mm. Further growth of age group I can be followed by tracing the modes from July 1953. There is a mode of 197 mm in July 1953 and by October a modal length of 222 mm was obtained.

*Age group II.*—The growth of the age group II cannot be identified satisfactorily in the length-frequency distributions because of inadequate samples.

Many attempts have been made previously to determine the age of the spot by length-frequency polygons (Welsh and Breder, 1923; Hildebrand and Schroeder, 1928; Pearson, 1928; Hildebrand and Cable, 1930; Townsend, 1956; Pacheco, 1957; and Dawson, 1958). Dawson (1958) summarized the conclusions of various authors.

Pearson (1928) stated that the young-of-the-year from the Texas coast reached a total length of 130 mm by the end of October. Age group I had a modal length of 190 mm in April and showed very little growth. By November and December age group I spot migrated from bays to the Gulf of Mexico for spawning and did not return to the bays in the spring in sufficient numbers. A similar migration occurs in Lake Pontchartrain. The age group 0 spot is the most abundant age group in the lake and they move out of the lake into the Gulf of Mexico by November and December. Age groups I, II, and III spot also move out of the lake into the Gulf of Mexico by November and December, presumably for spawning. No attempt was made to determine the age of spot at maturity. Catch statistics indicate that no spot were taken during December (Suttkus, Darnell, and Darnell, 1954) and this appears to be a case of complete withdrawal of spot from the lake. Age groups II and III are not well represented in the samples from Lake Pontchartrain. A tagging program might yield interesting information on the movements of spot.

Welsh and Breder (1923) assigned a modal length of 140 mm to one year old spot at Fernandina, Florida.

Hildebrand and Cable (1930) studied the growth of spot in the first year. The young-of-the-year appeared in December and by the following November they had attained a total length of 139.3 mm.

Townsend (1956) stated that at an approximate age of one year the spot in Alligator Harbor, Florida, range from 122.8 to 166.8 mm in total length.

Dawson (1958) reported that most South Carolina spot attain between 148.7 to 168.1 mm in total length in their first year. Spot in their second year of life attained between 213.3 to 226.2 mm in total length.

Spot in Lake Pontchartrain attained a modal length of 142 mm at the end of the first year of life; growth of the subsequent age groups is not clear because of insufficient samples.

## Summary and Conclusions

This report presents the results of age and growth studies on the spot, *Leiostomus xanthurus* Lacépède, from the Lake Pontchartrain area, Louisiana.

A total of 1,418 spot collected by various methods were used in this investigation. The following conversion ratios were calculated. Between 19 and 49 mm in total length a ratio of 1:0.816 for conversion of total length into standard length. Between 50 and 270 mm a ratio of 1:0.773 for conversion of total length into standard length.

Age and growth of the spot were determined primarily by scales and otoliths but were verified by the length-frequency method.

Spot scales are ctenoid and only one annulus is formed during February and early March each year. New radii often start at an annulus, but a few exceptions were also observed. Nevertheless, the origin of radii may be used as a supplementary guide for the location of an annulus.

Scales made their appearance when the total length of the body was 22 mm.

The relationship between total length and scale radius was determined from measurements of 1,418 spot. The relationship was linear and can be described by the equation $Y = 0.98693X + (-18.333)$.

Fraser's formula was used to back-calculate lengths at previous ages. Spot averaged 143.8 mm at the end of the first year of life, 200.1 mm at the end of second year, and 223.2 mm at the end of third year. The average annual increments were 143.8 mm during the first year, 48.6 mm during the second year, and 24.1 mm during the third year. Increase in length is greatest during the first year and thereafter the growth rate slows down. There was fairly good agreement on calculated growth of fish of the same and different age groups in different years' collections. The length attained at the end of first year of 1958-59 year collection was smaller when compared to that of previous years' collections. Further work will be necessary to determine the nature of factors responsible for slow and fast growth.

Growth of various year classes in different calendar years was evaluated. The amount of growth made by fish in a particular year of life varied from year to year.

An attempt was made to establish a relationship between the number of circuli and the age of the fish. On the average 132.1 circuli are laid down from focus to first annulus, about 38.3 circuli from first to second annulus, and about 20.1 between second and third annuli. The number of circuli may be used to determine the approximate age of spot in fractions of a year. Caution must be exercised in applying this method because the variations in the range are considerable. However, the number of circuli, like the radii, can be used as a supplementary guide to locate an annulus.

The longest specimen was 270 mm in total length, had attained the age of three, and was in its fourth year of life. The vast majority of the spot probably die or migrate after attaining an age of two years. This is evidenced by the fewer number of spot in age group III.

Each otolith has a centrally located nucleus surrounded by alternating bands of opaque and translucent areas. The growth marks are clearly visible on the concave side of the otolith. The annulus which represents winter growth appears as a translucent band and the region in between two annuli which represents summer growth appears opaque in reflected light. Only one annulus is formed each year during late January and February.

The relationship between total length and otolith radius was determined from measurements of 1,064 spot. The relationship was linear and can be described by the equation: $Y = 0.16438X - 9.4418$.

The calculation of intermediate lengths was accomplished by using the direct proportion equation. Spot averaged 153.3 mm

at the end of their first year of life, 212 mm at the end of their second, and 225.1 mm at the end of their third.

There was general agreement between the scale year marks and otolith year rings from the same fish. Parallel age determinations by scales and otoliths were made for 1,064 spot. The calculated lengths based on scales and those based on otoliths coincide closely, thereby indicating that either may be used for age determination in the spot.

The length-frequency distributions of the spot show the growth of the young-of-the-year very well. They attain a length of 142 mm by January. This closely corresponds with the calculated lengths based on scales and otoliths. Comparison of the monthly station samples of the young-of-the-year spot showed that there was a difference in mean total lengths for spot taken from various stations. Apparently, young spot group in the lake after their entry and remain more-or-less as discrete populations through spring and summer. Growth of age group I can also be traced, though incompletely, in the length-frequency distributions. Growth of age group II cannot be identified satisfactorily because of insufficient samples.

## Acknowledgements

I am indebted to Dr. Royal D. Suttkus, Tulane University, for suggesting the problem, for his interest, guidance, and use of his extensive data on the spot.

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## Abstract

Age and growth of the spot, *Leiostomus xanthurus* Lacépède, from Lake Pontchartrain area, Louisiana, were determined by the scale and otolith methods and verified by length-frequency method. For the study 1,418 spot obtained by various methods in 1953-54, 1955, and 1958-59 were used. Annuli on scales and otoliths were formed during February and early March. The maximum annual increase in length occurred during the first year. Thereafter, the growth rate decreased. An attempt was made to establish a relationship between the number of circuli and the age of spot. The longest specimen was 270 mm in total length and had attained the age of three and was in its fourth year of life. There was good agreement between scale year marks and otolith year rings from the same fish. The calculated lengths based on scales and those based on otoliths coincide closely, thereby indicating that either may be used for age determination in the spot. The length-frequency distributions of the spot show the growth of the young-of-the-year very well. Young spot taken at various stations in the lake exhibited differences in the growth rate. Presumably, young spot group in the lake after their entry and remain as more or less discrete populations through spring and summer. Growth of age group I could be traced, though incompletely, whereas growth of age group II could not be traced in the length-frequency distributions because of inadequate samples.

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# TULANE STUDIES IN ZOOLOGY

Volume 8, Number 3 December 2, 1960

## THE BREEDING HABITS OF THE MOLE SALAMANDER, *AMBYSTOMA TALPOIDEUM* (HOLBROOK), IN SOUTHEASTERN LOUISIANA

C. ROBERT SHOOP,

*DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY*
*NEW ORLEANS, LOUISIANA*

## SALINITY RELATIONS OF SOME FISHES IN THE ARANSAS RIVER, TEXAS

WILLIAM C. RENFRO,

*U. S. BUREAU OF COMMERCIAL FISHERIES,*
*BIOLOGICAL LABORATORY,*
*GALVESTON, TEXAS*

TULANE UNIVERSITY
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# THE BREEDING HABITS OF THE MOLE SALAMANDER, *AMBYSTOMA TALPOIDEUM* (HOLBROOK), IN SOUTHEASTERN LOUISIANA[1]

C. ROBERT SHOOP,
*Department of Zoology, Tulane University, New Orleans, Louisiana*

Various aspects of the breeding habits of several ambystomatids[2] in the northern United States have been described. Knowledge of the reproductive activities of the species of *Ambystoma* endemic to the Southeast remains fragmentary. Only the eggs and time of breeding of *Ambystoma talpoideum* have been described. Much of the literature dealing with the mole salamander reports only the occurrence of the form in one or more localities.

In the region studied, freezing temperatures are infrequent, and seasonal variations of moisture limiting the activity of salamanders are less pronounced than those in most other parts of the country. Studies of the behavioral and ecological isolating mechanisms, of which courtship patterns may be a part, of the sympatric species of *Ambystoma* in the Southeast are needed to understand better their phylogenetic relationships. The purpose of this study was to obtain detailed information of the breeding behavior of *Ambystoma talpoideum* in southeastern Louisiana.

Studies of the breeding habits were conducted both in the field and in the laboratory from October, 1957, through March, 1959. Occasional visits were made to the field area during the winter of 1959-60.

## Materials and Methods

Juvenile and adult *Ambystoma talpoideum* were collected by seining and dip-netting in ponds and ditches and random turning of sticks, logs, paper, and boards on land. Immediately before ponds filled with water, adults in breeding condition were captured by raking the moist floor of the pond depression by hand. During the breeding season of 1959-60 specimens were collected with the aid of a 230 V. AC electrical shocker. This was the most efficient method of collecting.

Two standard temperature readings were made during each visit to the breeding ponds: (1) air temperature 1 meter above the surface, and (2) water temperature (water 10 cm in depth). When specimens were found on land, ground surface temperatures were recorded at the exact location of capture.

A United States Weather Bureau Cooperative Observer Station, at Slidell, St. Tammany Parish, Louisiana, close to the study area, provided useful climactic and weather data.

Measurements of total length, body length, and tail length were made with the aid of vernier calipers. An ocular micrometer on a dissecting microscope was used for measurement of eggs and spermatophores.

The distance from the tip of the snout to the posterior end of the cloacal aperture constitutes the body length; tail length is the distance from the posterior end of the vent to the tip of the tail. Each measurement is estimated to be accurate within 1.5 mm.

Specimens collected during the 1957-58 breeding season were killed in ten percent formalin before hardening and preservation. Those collected and preserved during the 1958-59 and 1959-60 seasons were killed in ten percent isopropyl alcohol before preservation. All specimens were hardened and preserved in eight percent formalin. Representative series collected during this study have been placed in the Tulane Collections.

The ovaries of gravid females consist almost entirely of mature ova. Counts of ova were made in excised ovaries. The ova were carefully teased from the ovary, counted with the aid of a hand tabulator, and deposited in the Tulane Collections.

Night observations were made with the aid of bright and dim flashlight illumination, both in the field and in an outdoor concrete pit on the Tulane campus. The entire courtship activity was observed using a dim

[1] Awarded the Stoye prize as the best student paper in Herpetology at the 40th annual meeting of the American Society of Ichthyologists and Herpetologists.

[2] For usage of the emended Ambystomatidae rather than the conventional Ambystomidae, see Tihen (1958:1 footnote).

flashlight, the lens of which was covered by red cellophane simulating the photographer's red light used by many authors in observing the courtship dances of salamanders (*cf* Kumpf and Yeaton, 1932).

A single natural study area was utilized for this investigation. It is designated "Siren Ponds", and is in St. Tammany Parish, Louisiana, three and one-half miles west-northwest of Slidell, at about ten feet above sea level. The area consists of two separate ponds adjacent to a road. The larger pond, North Siren Pond, reaches a size of 30 by 25 meters and a depth of about 1.5 meters at full capacity. The smaller pond, located about 30 meters south of North Siren Pond is designated as South Siren Pond and is L-shaped, measuring approximately 15 meters in length and 10 meters on the shorter leg. South Siren Pond varies from one to four meters in width and up to one meter in depth during high water.

During the summer and fall of 1958 large portions of North Siren Pond were destroyed or disturbed by roadbuilding operations. Several mole salamanders collected during the 1959-60 breeding season exhibited body damage and regenerated limbs and tails indicating that the disturbance affected at least a portion of the population. The roadbed, composed primarily of clay, erodes during rains, and the water throughout most of this pond in early 1959 was extremely murky. Water samples kept undisturbed in the laboratory required over a month to settle.

Within and around North Siren Pond proper are live oak (*Quercus virginiana*), sweet gum (*Liquidambar styraciflua*), and southern hackberry (*Celtis mississippiensis*) trees. Within and around South Siren Pond are loblolly pine (*Pinus taeda*) and a few small sweet gum. The land surrounding the ponds is heavily forested with loblolly pine. Dead pine needles cover the floor of the forested area in some places to a depth of almost a meter. Few shrubs are present, although greenbrier (*Smilax* spp.) is present in large colonies. Grasses are present in the more open areas. Burrowing mammals and their extensive tunnels are found in the decaying pine needles. The small burrows are probably constructed by shrews, (*Blarina brevicauda* and *Cryptotis parva*) and cotton mice (*Peromyscus gossypinus*). Other mammals present in the area are skunks (*Mephitis mephitis*), opossums (*Didelphis marsupialis*), swamp rabbits (*Sylvilagus aquaticus*), and gray squirrels (*Sciurus carolinensis*).

Within the two ponds is a variety of poikilothermic vertebrates including siren (*Siren intermedia*), newts (*Diemictylus viridescens*), green frogs (*Rana clamitans*), leopard frogs, (*Rana pipiens*), cricket frogs (*Acris gryllus*), chorus frogs (*Pseudacris triseriata*), mud turtles (*Kinosternon subrubrum*), pigmy sunfish, (*Elassoma zonatum*), and mosquito fish (*Gambusia affinis*). At times of overflow, black bullheads (*Ictalurus melas*) and very small largemouth bass (*Micropterus salmoides*) are present. Fairy shrimp, crawfish, back swimmers, diving beetles, leeches, and other invertebrates are common.

Many observations were conducted in a rectangular concrete pit 2.32 by 1.52 meters and 0.68 meters deep on the Tulane campus. Water depth was varied to suit the particular experiment. The sides were vertical and the floor sloped slightly to a drain. An overflow drain prevented the water level from rising above 0.53 m. A certain amount of debris (sticks, twigs, catkins, and leaves) continually fell into the pit.

Aquaria of several sizes were utilized for laboratory studies. Water in the aquaria was filtered and aerated. Fine gravel was used as a substrate with *Anacharis* sp. as the only vegetation. The room in which the aquaria were kept was 20° C. ± 2°.

## Results and Discussion

### *Breeding Season*

*The breeding period.*—Professor F. R. Cagle (personal communication) recorded breeding of *Ambystoma talpoideum* from early December until the middle of February for the years 1949 through 1955 at the Siren Ponds. Gentry (1955) remarked that *A. talpoideum* deposits eggs during January or February in Tennessee. Allen (1932) witnessed *A. talpoideum* "breeding" in Henderson County, Mississippi on February 12, 1930. Carr (1940) collected breeding adults in Alachua County, Florida on February 14, 1933. Mosimann and Uzzell (1952) found breeding adults in Dorchester County, South Carolina on December 31, 1951. Apparently throughout the greater portion of its

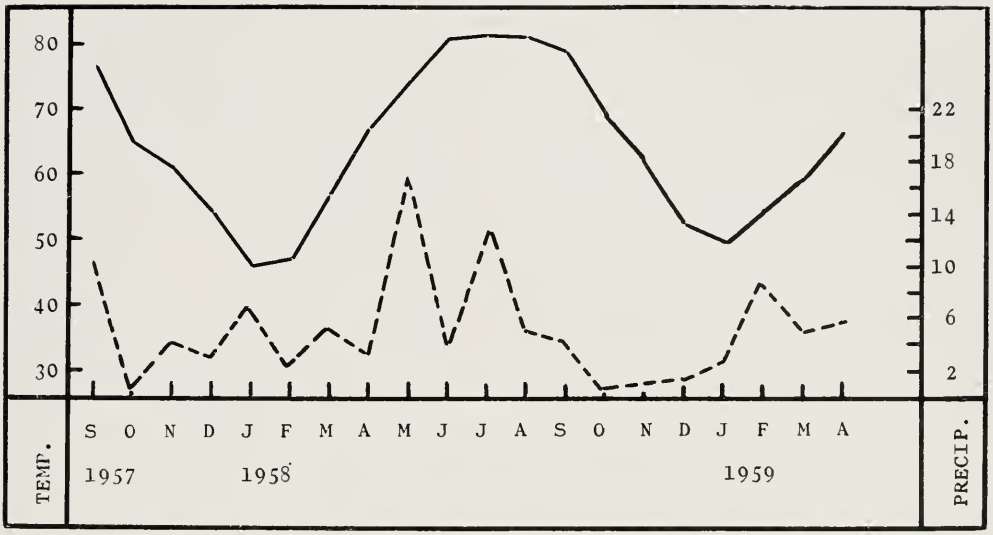


Figure 1. Average monthly temperature in degrees Fahrenheit (solid line) and total monthly precipitation in inches (dashed line) from September, 1957 to April, 1959 as recorded by the U. S. Weather Bureau at Slidell, Louisiana.

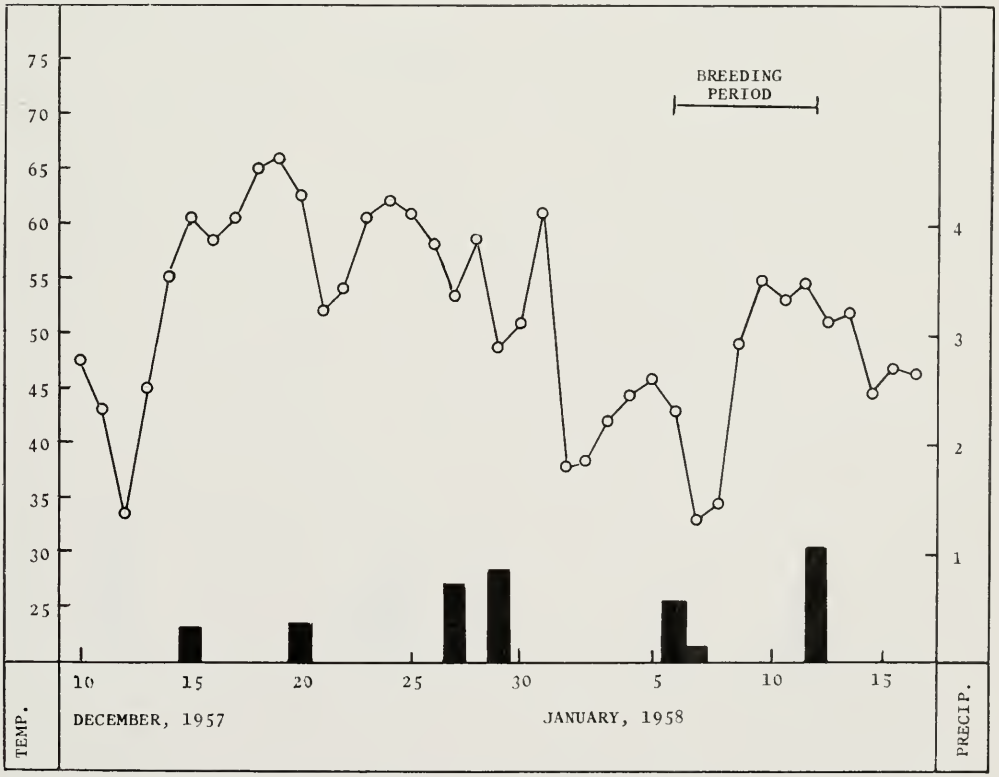


Figure 2. Average daily temperature in degrees Fahrenheit (solid line) and total precipitation in inches (darkened columns) recorded at Slidell, Louisiana, for the period December 10, 1957, through January 17, 1958. The breeding period of *Ambystoma talpoideum* is indicated.

range, the mole salamander is a winter breeder, although the length of an individual breeding period has not yet been reported.

In 1958, breeding activity in the Siren Ponds began on or about January 6, as judged by the appearance of eggs found on January 8. This breeding period ended by January 12, when intensive efforts to collect mole salamanders in the ponds were fruitless. Thus the reproductive activity apparently covered a span of seven days. The breeding period of 1959 lasted for eight days, January 30 to February 6. Breeding adults were found in North Siren Pond on January 8, 1960. On January 23, 1960, two adult mole salamanders in breeding condition were located by the electrical shocker in the same pond, indicating a possible breeding period of 15 days.

*Climatic factors influencing the breeding period.*—Weather conditions during the two breeding seasons of this study varied considerably. A relatively large amount of precipitation throughout the late summer and fall of 1957 filled the ponds by November 1957. Precipitation was relatively sparse in the late summer and fall of 1958 (fig. 1); no water was present in the ponds until January 30, 1959. The average air temperatures during the first fall and winter of this study were lower than those a year later (fig. 1).

On December 30, 1957, there were no salamanders in the pond or under logs surrounding the pond. Rains had occurred one and three days previously, and temperatures were relatively warm during those rains (fig. 2). Precipitation occurred on January 6 and 7, 1958 with accompanying cold temperatures; breeding activities began at this time.

As soon as the ponds began to fill in 1959, and lower temperatures and rains coincided, breeding took place (fig. 3). Water and air temperatures in 1959 were higher

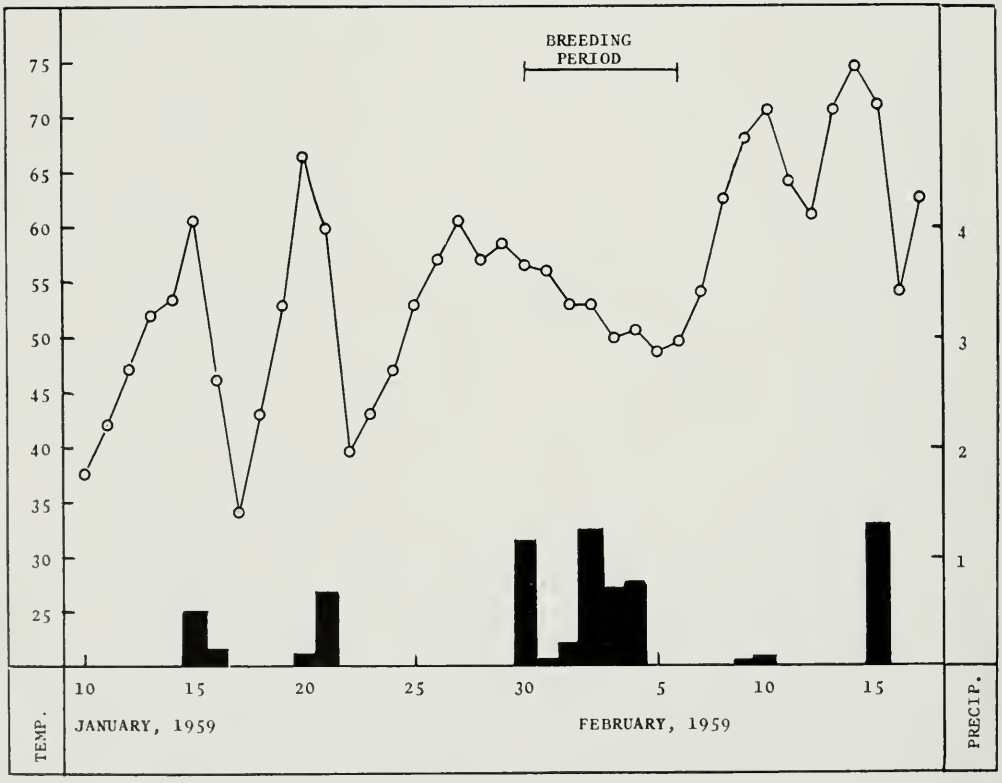


Figure 3. Average daily temperature in degrees Fahrenheit (solid line) and total daily precipitation in inches (darkened columns) recorded at Slidell, Louisiana, for the period January 10, 1959, through February 17, 1959. The breeding period of *Ambystoma talpoideum* is indicated.

TABLE 1.

*Summary of collections at the Siren Ponds during the breeding seasons of 1957-58 and 1958-59*

| Date | Number of Males Collected | Number of Females Collected | Total Adults Collected | Time (PM) | Temperature °C Water | Temperature °C Air | Water Depth (in cm) |
|---|---|---|---|---|---|---|---|
| Dec. 30, 1957 | 0 | 0 | 0 | 8:15-9:00 | 16.0 | 14.0 | 30 |
| Jan. 8, 1958 | 2 | 1 | 3 | 8:30-9:30 | 4.5 | —1.1 | 58 |
| Jan. 9, 1958 | 2 | 1 | 3 | 8:00-9:30 | 6.0 | 2.5 | 58 |
| Jan. 10, 1958 | 12 | 11 | 23 | 7:30-8:30 | 7.0 | 6.5 | 60 |
| Jan. 11, 1958 | 6 | 4 | 10 | 5:30-7:15 | 10.0 | 11.0 | 60 |
| Jan. 12, 1958 | 0 | 0 | 0 | 8:30-9:30 | 11.0 | 15.0 | 73 |
| Jan. 13, 1958 | 0 | 0 | 0 | 8:30-9:30 | 12.0 | 15.5 | 79 |
| Total 1957-58 | 22 | 17 | 39 | | | | |
| Jan. 30, 1959 | 11 | 5 | 16 | 8:00-9:20 | 15.5 | 12.5 | 15 |
| Jan. 31, 1959 | 2 | 1 | 3 | 3:00-4:30 | 15.5 | 15.0 | 15 |
| Feb. 2, 1959 | 2 | 6 | 8 | 8:30-9:30 | 10.5 | 11.5 | 22 |
| Feb. 4, 1959 | 25 | 11 | 36 | 8:20-9:20 | 9.0 | 7.0 | 25 |
| Feb. 6, 1959 | 2 | 1 | 3 | 8:30-9:20 | 11.0 | 11.0 | 26 |
| Feb. 8, 1959 | 0 | 0 | 0 | 5:45-7:00 | 18.5 | 22.0 | 15 |
| Total 1959 | 42 | 24 | 66 | | | | |

than those during breeding activities in 1958. The largest collection of individuals during one evening in 1959 occurred when the water temperatures were the coldest of the year and approached those of the previous year (Table 1).

The factors constituting a stimulus to breeding in southeastern Louisiana are complex. Heavy rains and lower temperatures apparently interplay in stimulating the breeding of *A. talpoideum* (figs. 2, 3). During the breeding season of the years 1957 through 1960, moderate to heavy rains were associated with breeding activity. If low temperature is unimportant, the heavy rains of December 27 and 29, 1957, should have been sufficient stimulus for breeding to occur. At that time, temperatures were seasonally normal and the ponds contained water. No breeding activity resulted, but when rains and relatively cold temperatures coincided (January 6, 7, 1958), breeding commenced (fig. 2). During the winter of 1958-59, when the ponds were unseasonably dry, breeding was delayed until water was present. When breeding occurred, the temperatures were not as low as those of the previous year. This observation would seem to indicate that only cool temperatures are needed, or that the lack of water in the ponds forced the adults to utilize conditions which were not optimum.

*Breeding Adults*

*Males.*—The cloacal region of the male swells and becomes protuberant (figs. 4, 5) during the breeding season. The tail becomes finned (as in other ambystomatids), and the tip of the tail is oar-shaped. A rough, glandular appearing area located dorso-laterally on the tail is prominent. Salamanders kept in the concrete pit after breeding lost the pronounced tail fin within one to two weeks. The cloacal swelling recedes after one to three weeks.

Of 88 males from the breeding pond, the largest specimen (T.U. 13589.5) collected in North Siren pond during the breeding season, was 122 mm in total length (body 66).[3] The smallest breeding male was 83 mm in total length (body 48). The body lengths of 88 breeding males varied from 48 to 68 mm (mean, 57.2 mm). The tail lengths of 83 males made up 38 to 47 per cent of the total length (range, 33 to

[3] The tail is somewhat fragile and was broken or injured in several individuals. In starved animals or adults collected in seasons other than winter, and having no fin, the tail is proportionately smaller than in breeding adults. For these reasons, I consider body length a more valid measurement than total length. However, total lengths and tail lengths are presented for comparisons with measurements given by other authors.

Figure 4. Dorsal view of two *Ambystoma talpoideum* in breeding condition. Left, female; right, male.

Figure 5. Ventral view of two *Ambystoma talpoideum* in breeding condition. Left, female; right, male.

56 mm; mean 42.7 mm) (fig. 6).

*Females.*—A slight swelling of the cloacal region is evident in the breeding female, although the amount of protuberance is much less than that of the male (figs. 4, 5). The tail fin is somewhat pointed at the distal end. A dorso-lateral glandular area on the tail, such as found on males, is much reduced. If the adult is kept in water the fin is lost within one to two weeks after courtship.

Of 52 females from breeding aggregations in the Siren Ponds, four had a total length of 111 mm, the maximum for this series (mean, 96.6 mm). The smallest total length was 81 mm (body 46). Body lengths of the females ranged from 46 to 67 mm (mean, 59.5), and tail lengths ranged from 33 to 48 mm (mean, 41.0 mm) constituting 37 to 46 per cent of the total lengths.

*Sizes of males and females combined.*—The mean total length of 135 breeding adults (83 males and 52 females) was 99.5 mm and the mean tail length was 42.0; the average body length of 140 breeding individuals (88 males and 52 females) was 58.0 mm. The maximum total length of adults according to Bishop (1947) is 97 mm; Conant (1958) noted "3 to 4 inches." Many individual *A. talpoideum* measured during this study were considerably larger. The male measuring 122 mm in total length represents a record size for the species. The size range of both males and females is great (fig. 6), perhaps indicating that breeding populations may be composed of several age groups.

*Coloration.*—Coloration of any individual may change during a given period of time. When the adults are removed from the breeding pond, a color pattern is barely discernible. The back and sides are liver color with light flecks, fading into blue-gray on the ventrum. If kept in captivity for some time, the animal becomes blue-gray dorsally and lichen-like markings develop on the dorsum. Except on very young specimens, a light brown or tan area is present on the dorsum of the tail and occasionally on the back of the head. Young specimens invariably have a dark median stripe on the belly.

### *The Breeding Aggregation*

*Composition of the breeding aggregate.*—All specimens collected within the ponds during the breeding season were sexually mature. One sexually immature individual was collected near the ponds during the breeding season.

No distinct size groups can be seen in this sample, although the smallest individuals are probably young adults breeding for the first time. Many of these young adults possess vestiges of the larval belly pattern (*i.e.* a dark median belly stripe). The finding of a single immature specimen during breeding season indicates that at least some of these salamanders do not breed during the first breeding season following metamorphosis.

Males are more common in the breeding ponds at the onset of reproductive activities. They may continue to be more numerous than females throughout most of the breeding period (Table 1). Spent females were observed leaving the pond during the breeding period, showing that females leave the breeding pond soon after laying their eggs. Males apparently remain for the entire period. Undoubtedly, both males and females continue to enter the pond throughout this time. Non-continuous sampling of the breeding population might give erroneous indications of the sex ratio. Blanchard (1935) emphasized that in the determination of the relative numbers of the sexes, exclusion of adults is necessary because of differences in habits, and only juveniles should be used for the determination.

*Behavior of individuals in the breeding aggregation.*—Twenty days prior to the breeding activities of 1959, one male was collected under a board near North Siren Pond. There had been rain two days earlier, but no water was present in the pond. During a light rain ten days later three males and two females were found in the moist floor of South Siren Pond. Evidently the adults are near the ponds before reproductive activities commence, and during unusually dry winters, they presumably may burrow in the pond floor prior to the breeding period.

Individuals in the breeding pond often burrow in the debris covering the floor during daylight hours. At night, they may be found in every part of the pond; no dis-

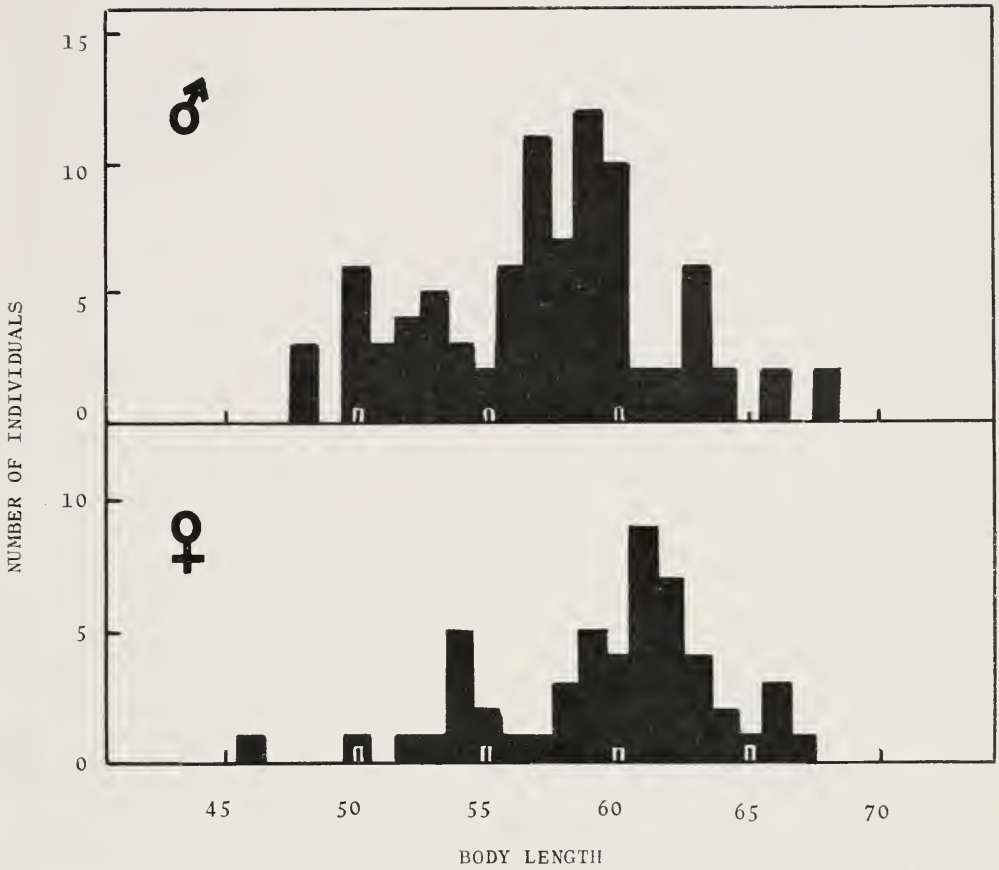


Figure 6. Body lengths of 88 males and 52 females in breeding condition. Measurements are in mm.

tinct preference is shown for a certain depth of water. A congregation of females was detected during the breeding period of 1958 in a region of the pond where large numbers of twigs and sticks were located. These females were probably laying eggs in this region.

All individuals invariably shy from the light of a flashlight if they are not courting. Adults in captivity attempt to hide during the day.

Lower temperatures are apparently preferred for breeding purposes (figs. 2, 3). The largest concentration of adults was found when water temperatures were lowest. No breeding adults were found in the ponds in water warmer than 16° C (Table 1), although warmer water was utilized for breeding in captivity. Two spent females were collected from water with a thin ice coat near Hickory, Louisiana, on January 8, 1958.

### *Courtship Pattern*

Courtship was not observed in the field. On January 30, 1959, two pairs were found following each other about the edge of the pond. Subsequently, four males and four females collected on this date and kept refrigerated until February 3, were placed in the concrete pit on the Tulane campus. Water depth ranged from 4 to 22 cm due to the slanting floor. The water temperature was 17° C. A small amount of debris consisting of leaves, twigs, larger sticks, a concrete block, and a brick was scattered about on the floor of the pit. Observations from 7:00 PM to 9:30 PM using a dim flashlight showed no courting activity. The individuals seemed to shy from the light. At 8:00 AM the following morning, two

clusters of eggs, containing 11 and 13 eggs, respectively, were found on a small twig in the deepest water. By 3:30 PM, 18 more eggs were found on leaves and on the bottom of the pit. Occasionally the adults would move about and swim to the surface to gulp air. At 8:00 AM on February 5, the debris on the floor, and the walls were covered with small clusters of from 2 to 22 eggs. Spermatophores were common on the floor; ten spermatophores were collected, measured, and preserved. This was the first indication that captive specimens would court. During the evening of February 6, the egg laying of several females was observed.

At noon on February 7, all eight salamanders were removed from the pit. At this time two females collected on January 30 and 31, and kept in a refrigerator at 6° C., were placed in the pool. Two males, which had been kept in the pit previously and two males collected January 30 and kept at 6° C. since capture, were released in the pit at 6:15 PM. A dim flashlight covered with red cellophane was used to observe these salamanders continuously from 6:15 until 10:00 PM. No unusual movements were observed until 7:15 PM. At this time a male began bumping the head of a female with his snout. Air temperature at this time was 17° C while the water temperature was 14° C. From this time until observations ceased at 10:00 PM, courtship activity occurred almost continuously. Nine separate courtship dances were observed during the evening of February 7. Only two dances resulted in sperm transfer.

All spermatophores were removed from the pit the morning following observations of the dances. No subsequent spermatophores were found in the pit, indicating that courtship, at least of the females in the pit, had ended.

On February 20, ten pairs of adults collected on February 4, and kept refrigerated, were placed in the pit to verify previous observations and to provide eggs for future studies of larvae. On removal February 27, only 14 individuals were in the pit. The tail fin was reduced in all of them and the cloacal swelling of males was lessened. All six missing individuals were females.

*Courtship.* — After bumping the female for about 10 seconds (fig. 7A), the male runs his head along the sides of the female to her cloacal region. The female begins nosing the cloacal region of the male and both of them push with their heads. This results in a circular movement or "waltz" of one or two revolutions (fig. 7B). The male here breaks contact with the female's cloacal region and begins to straighten his body. The female slides her head down to the tip of the male's tail. Thereupon the male begins a peculiar wagging of the pelvic region and proximal portion of his tail while keeping the posterior part of the tail undulating and often touching the female's head (fig. 7C).

At this time his cloacal aperture opens and the spermatophore stalk may begin forming. Using the front feet for propulsion the male moves forward slowly continuing the wagging motion. The female follows, keeping her head in contact or in close proximity to the male's tail. After one to eleven minutes of following, the female pushes her head along the male's tail until she reaches his cloacal region or hind legs. At this time she bumps the male (fig. 7D) on the cloacal region one or two times and the male ceases the pelvic movement. With the hind legs directed outward and posteriorly, the male deposits a spermatophore (fig. 8A). If he does not stop his movements, the female returns to the distal end of his tail. Immediately after deposition the pelvic motion is resumed. The female noses the spermatophore and slowly begins to crawl over it (fig. 8B), the male keeping his tail near the female. If the female is led by the male to a position in which her cloaca is directly over the spermatophore, she will assume the same posture taken by the male in depositing the spermatophore and, using her cloacal lips, pick up the entire spermatophore or clip off the sperm cap (fig. 8C). Rarely does the male so lead the female. If the female successfully picks up a spermatophore or cap, immediately after or within a minute or so, she loses interest in the male and wanders away from him (fig. 8D). The male continues his wagging movements for several minutes. If a successful pickup is not made, the female continues to follow the male until such occurs or until the dance is terminated, usually when the pair becomes separated. One female was ob-

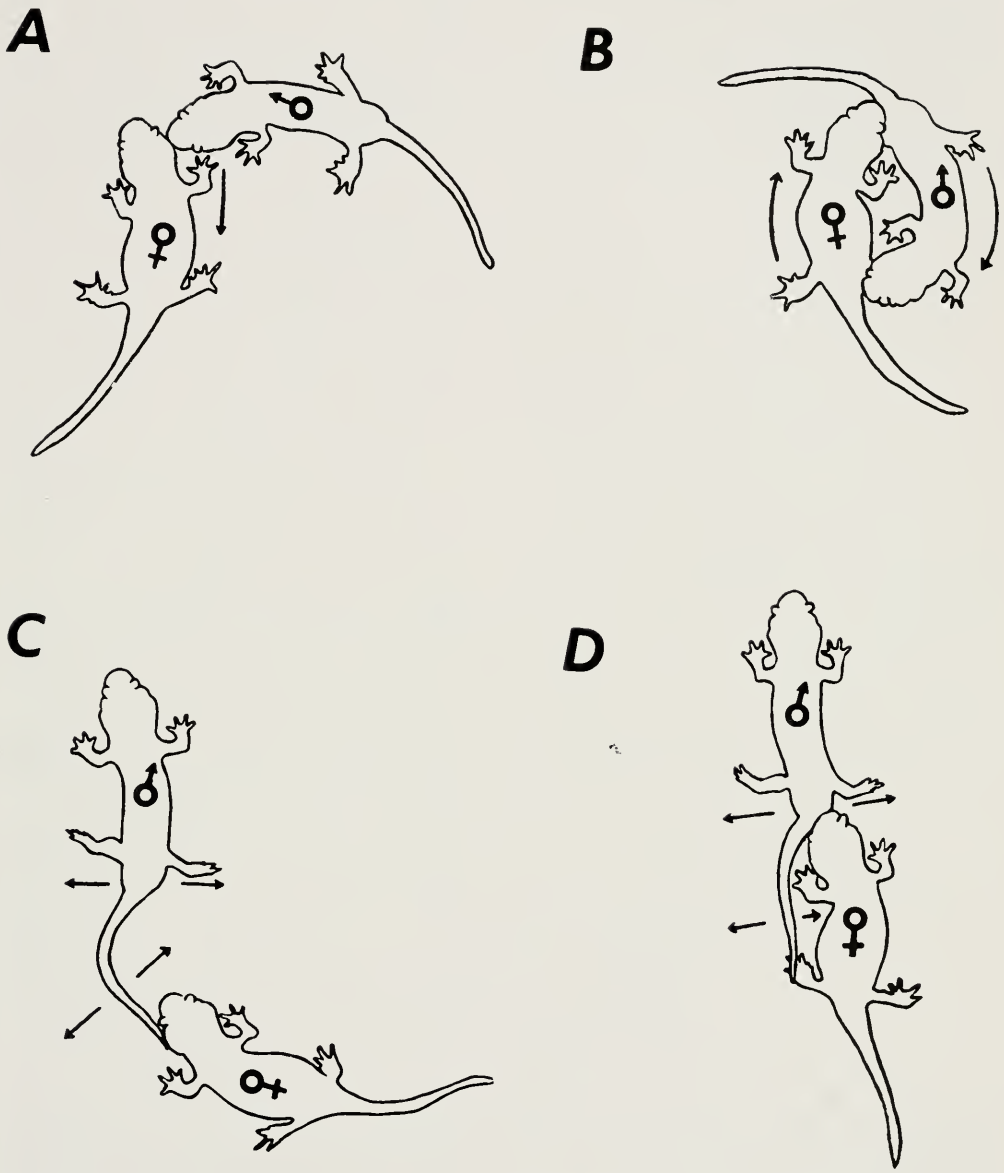


Figure 7. Courtship pattern of the mole salamander. **A**, male noses female; **B**, the "waltz"; **C**, female follows male; **D**, female bumps the cloaca of the male.

served to be unsuccessful in seven attempts to pick up a spermatophore, finally leaving the male courting her. The pair moved a distance of over seven feet during this courtship dance. A female may be courted by many males and offered many spermatophores before she picks one up. Females will pay no attention to spermatophores unless they are offered during courtship.

At times another male may join the dance and will push between the original male's tail and the female's head, thereby separating the pair engaged in the dance. The intruder then begins courtship by bumping the head of the female and following the above pattern. In this case, the rejected male continues the pelvic motion for some minutes. Use of a weighted sponge with

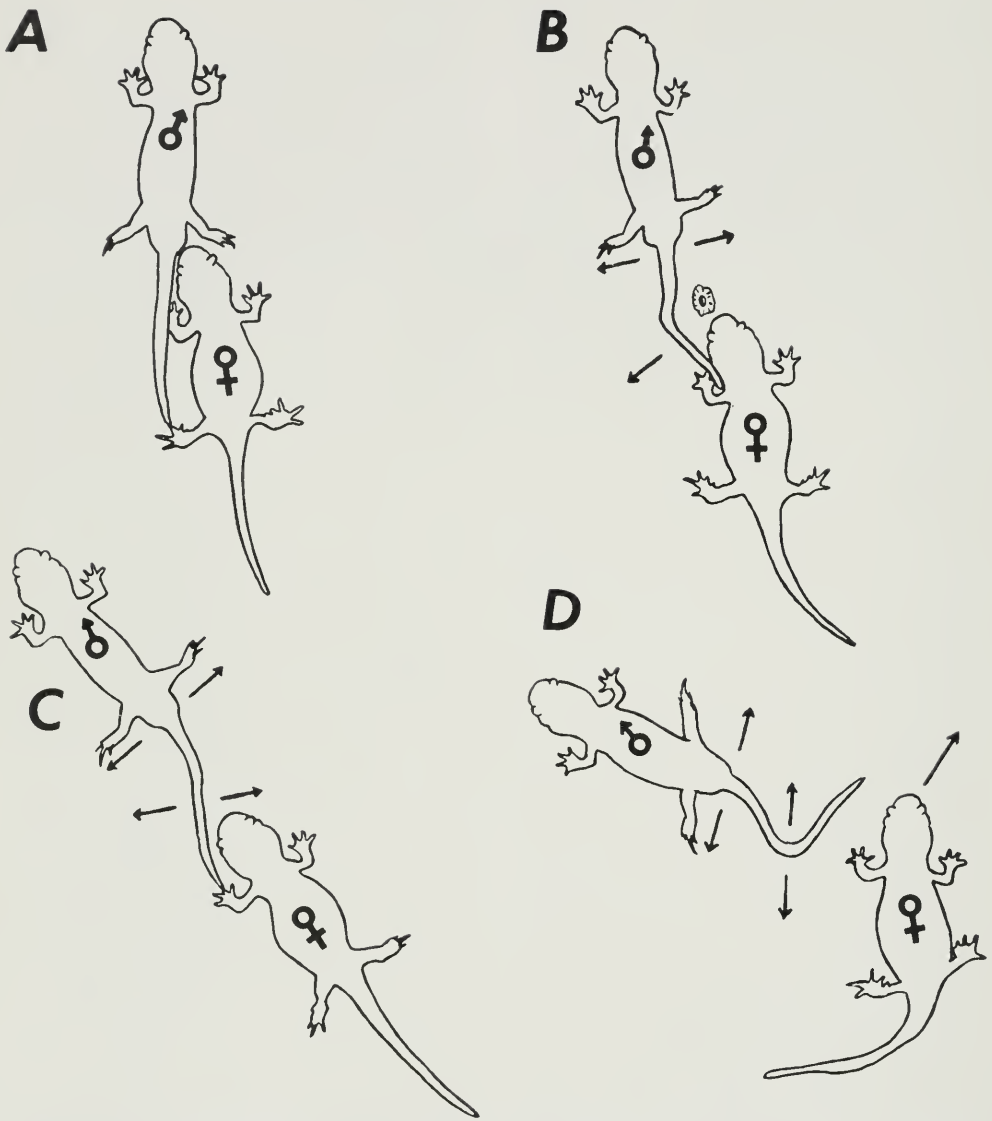


Figure 8. Courtship pattern of the mole salamander. **A**, male deposits a spermatophore; **B**, female noses spermatophore; **C**, female picks up spermatophore or spermatophore cap; **D**, female leaves male.

female secretions in the manner described by Twitty (1955) yielded no results. Apparently, meeting of the males and females is haphazard.

Total time for courtship dances ranged from seven to thirty-seven minutes. The shorter dances may have been terminated because of the use of flash bulbs in photographing the courtship.

*Effect of light.*—Dim light (red or white) has little effect on the courting individuals. Bright light will cause the participants to stop all movement. If the bright light is removed quickly, the courtship will continue. Any light, no matter how dim, may cause non-courting individuals to shy away.

### *Spermatophores*

A male placed in an aquarium at 20° C without females deposited two spermatophores, indicating that courtship is not necessary for deposition. Males injected with

four female *Rana pipiens* pituitaries, as suggested by Noble and Richards (1932), began depositing spermatophores within 48 hours. The total observed number of spermatophores produced during courtship by an uninjected male was fifteen.

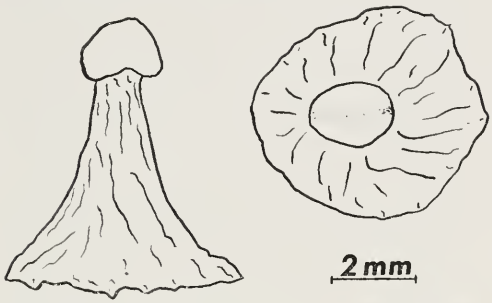


Figure 9. Spermatophore of *Ambystoma talpoideum*. Left, side view; right, top view.

The spermatophore has a wide circular base with a relatively thin stalk tipped by a sperm cap (fig. 9). All spermatophores were attached loosely to the pool or aquarium floor. The jelly-like base is clear and gelatinous, while the sperm cap is cottony white. The general shape of the cap is a flattened ellipsoid, but is variable and may be almost spherical. On the top, a slight fold runs from the anterior to the posterior end dividing the cap into two approximately equal halves (fig. 9). The jelly-like stalk has a blunt apex and a relatively wide base. The total height ranges from 6.3 to 8.5 mm; stalk length 3.6 to 6.6; base width 5.1 to 8.2; stalk at narrowest point 1.0 to 2.5; cap depth 1.0 to 2.6; cap length 2.6 to 3.1; and cap width 2.0 to 2.9.

Several spermatophores were examined microscopically the morning following deposition. The cap was found to be composed of cellular strands of two sizes. Apparently spermatozoa should have been found between these strands, but none was seen. Between the strands may be found extremely abundant colonies of protozoa (Sarcodina, Ciliata, and Mastigophora), vegetative hyphae of a phycomycete, and filaments and individual cells of green algae. The gelatinous stalk contains lesser quantities of these organisms.

### *Oviposition*

Courtship is not a necessary prelude to egg laying. Females collected on land before the breeding season may lay unfertilized eggs when placed in aquaria at room temperature (20° C). This phenomenon occurred with all three females tested, but Professor Cagle (personal communication) kept several gravid females in aquaria two months and oviposition did not result. A female placed in a terrarium containing only damp sand resorbed her eggs. The appearance of the ovaries of this female was essentially like those of *Ambystoma jeffersonianum*, described by Clanton (1934). Infertile eggs apparently are rare in nature as only one was observed. Under conditions in the concrete pit, several clusters contained one to many unfertilized eggs. Oviposition usually takes place at night, but one female was observed to lay eggs in the outside pit during a cloudy afternoon.

Eggs may be laid on any substrate in the breeding pond, but there is a decided preference for small twigs approximately one-eighth inch in diameter which are oriented at an angle to the surface. No definite preference was shown for a particular water depth. Areas containing many twigs and sticks seem to be preferred. Eggs were sometimes deposited on twigs near the surface of the pond at times of high water and, with the lowering of the water level, left hanging in the air.

Positions assumed during oviposition vary, depending on the substrate and its orientation in relation to the surface. If oviposition occurs on the bottom of the pit, the female assumes a position in which the cloacal lips are pressed firmly to the substrate and begins to wave the tail slowly. When the waving decreases or ceases one to several eggs may be deposited. If the female does not move during deposition, the form the eggs will assume after water absorption is a large spherical clump; if she moves slowly during deposition, using all four feet, the eggs will appear after water absorption as a long, single strand.

Several individuals have been observed laying eggs on the vertical walls of the concrete pit. The female's head is always pointed toward the surface and a grip on the roughened concrete is kept by all four feet. The tail undulates slowly before the initial deposition. The female appears to rest after laying one to six eggs; during this time, the tail waving is resumed. After

laying a clump of eggs the female returns to the floor of the pit.

If a twig is oriented at an angle to the surface of the water the female will swim up to the twig at a point about 10 to 15 cm from the floor, and grasp it with her hind legs. While waving her tail, she gradually turns under the twig with ventrum up. Using only the hind legs and feet for traction, she moves slowly along the twig toward the surface depositing eggs. The tail undulates slowly except during actual deposition. The trunk of the body may at times be nearly at a right angle to the twig. By alternately shifting the tail and body, and moving slowly between times of deposition, the eggs may be laid in a wave-like pattern along the underside of the twig. This method of laying was observed frequently, and many eggs in the natural pond because of their location on twigs appeared to have been laid in this fashion. Females do not always turn over to lay eggs on slanting twigs.

The eggs are laid in small clusters. Often many clusters appear on the same twig. These clusters may or may not be laid by one female. On one occasion a female was seen laying eggs between clusters of eggs deposited previously by another female. The number of eggs in 75 individual clusters ranged from one to 37. One marked female laid eggs during three consecutive nights in the concrete pit. More than one night is probably required for all the eggs to be laid. Two females took 15 and 22 minutes to lay 17 and 18 eggs, respectively, before returning to the bottom where they remained motionless for more than an hour.

*Eggs*

Only one series of adults collected on land before the breeding season is in the Tulane collections. This series (TU 13584), consisting of 33 specimens, was collected near the Siren Ponds on the same day, before water was present in the ponds. Fourteen are females containing enlarged ova within the ovaries. The number of ripe ova of each specimen varies from 226 to 401. From figure 10, one can see that the largest individual or the smallest did not produce the largest or smallest number of eggs, respectively. More data are needed to show a correlation, if any, between length and size

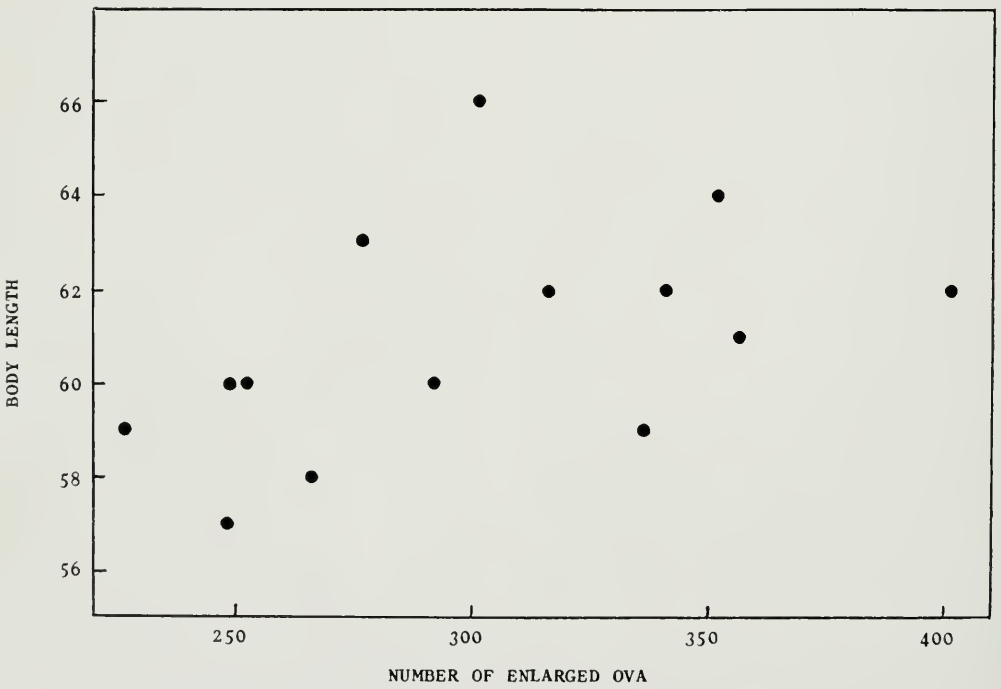


Figure 10. Graphical representation of body length in mm plotted against total number of enlarged ova.

of the egg complement. In no case was the number of ova in the two ovaries the same. Wilder (1924) showed in the salamander *Eurycea bislineata* that the number of large ova found in gravid females is consistent with the numbers of eggs deposited in the field.

The eggs and their envelopes are essentially as described by Mosimann and Uzzel (1952). Each is surrounded by a vitelline membrane plus two envelopes. A gelatinous covering or matrix is common to all eggs in a cluster. A sample of 25 fertile eggs deposited in captivity varied less than $\pm 0.4$ mm from the egg pictured by Mosimann and Uzzell.

## Discussion

*Breeding season.*—Blanchard (1930) and Baldauf (1952) indicated that adults of *A. maculatum* may be found in breeding ponds for a period of about two weeks or more, and that the salamanders move in waves to the pond because freezing temperatures and dryness often hinder the migration. *A. talpoideum* may spend considerably less time in the breeding pond.

Blanchard (1930) stated that rain and not temperature is the main stimulus to the breeding migration of *Ambystoma maculatum* in Michigan. He believed that rain occurring before the ground thaws, or daytime rains, would have no effect. In a footnote to Blanchard's paper, A. H. Wright wrote, "I regard the most necessary condition for each species as humidity above a more or less specific minimum temperature." Concerning *maculatum,* Bishop (1941), stated, "I would qualify this theory by adding that, in eastern New York, migration of this species and *A. jeffersonianum* may be initiated by rain during the day and even by the rapid runoff of snow water following a pronounced rise in temperature." Wright and Allen (1909) stated that an air temperature of 50° F or more was required to cause the emergence of *maculatum* from hibernation, whereas Baldauf (1952) claimed a slightly higher minimum of 55° F. Baldauf believed temperature and humidity to be the most important factors in stimulating the breeding migration of the spotted salamander. In all of the above considerations, temperature and moisture are considered important.

The role of temperature in the stimulation of the breeding of *talpoideum* may be opposite to that of *maculatum.* A warming trend after freezing temperatures is required by *maculatum,* but *talpoideum* apparently requires a cooling trend. Unfortunately, temperatures of water in the breeding ponds were not recorded by the previous authors. Since breeding takes place underwater, water temperatures would be of considerable value. Perhaps, either *maculatum* or other species of *Ambystoma* and *talpoideum* breed when the water temperatures are essentially the same.

*Courtship.*—The courtship of *Ambystoma talpoideum* differs from that described for several other eastern ambystomatids. Bishop (1941) observed the courtship of *Ambystoma jeffersonianum* in New York. The male grasped the female in an axillary embrace at the beginning of the courtship. Kumpf and Yeaton (1932) stated that the male then rubs the head of the female with his chin, undulates his body and tail, and eventually swims and walks ahead of the female to deposit a spermatophore. Before the spermatophore is released, the female applies her snout to the male's cloacal region. Mohr (1931) reported that *jeffersonianum* undulates the tail and body while depositing spermatophores.

Of *A. maculatum,* Bishop and others stated that the species often engage in a *Liebesspiel* upon arrival at the breeding site. Mohr (1931) believed the courtship of *maculatum* does not differ in important details from that of *jeffersonianum,* but Wright and Allen (1909) saw males rubbing the dorsal surface of their heads along the ventrum of the females. Following each performance of this kind the males swam away, deposited a spermatophore and returned to nose the females. Eventually the female picked up a spermatophore cap with her cloacal labia.

Noble and Brady (1933) found that a male *A. opacum* attempts to push his head under the cloacal region of a female, and the female does the same to the male. The pair may revolve in a circular movement which they described as the "waltz." The female may then pick up a spermatophore deposited by the male. The entire courtship takes place on land.

*Ambystoma tigrinum* is the most widely distributed member of the genus. Kumpf

(1934) has described the courtship dance of *tigrinum* in some detail. When depositing a spermatophore, this species raised the tail at right angles to the body. The female assumed the same posture when picking up the spermatophore. The male always pushed his head under the cloaca of the female before stalking ahead to deposit a spermatophore.

According to Tihen (1958) *A. talpoideum* is most closely related to *A. opacum.* These species may have arisen from the *maculatum* group stock. The vertebral proportions of *talpoideum* and *opacum* are intermediate between *tigrinum* and *maculatum,* however. Since *opacum* and *talpoideum* are closely related, one might assume that the courtship patterns would be similar, and indeed they are. The "waltz" of *opacum* is also executed by *talpoideum* at the beginning of the courtship. The undulating tail of the male, according to Noble (1931), is used to waft the secretions of the abdominal gland toward the female. Obviously, in a terrestrial situation such as that of *opacum,* this part of the courtship is impossible. If the recorded courtship patterns of *tigrinum* and *maculatum* are compared to those of *talpoideum,* many aspects of the courtship of the tiger salamander appear similar to that of *talpoideum.* Yet certain aspects of the courtship of *jeffersonianum* are also similar. More observations are needed to clarify the courtship differences of the *maculatum* and *tigrinum* groups.

Although female *talpoideum* exhibit difficulty in picking up spermatophores or spermatophore caps, the lack of infertile eggs in the breeding ponds shows the success of courtship activities. Extremely murky water in North Siren Pond in 1959 did not prevent successful courtship. Total potential reproductive capacity (as defined by Allee, *et al.,* 1959) of the breeding population appears to be almost realized, but the mortality rate of developing embryos and larvae may be high.

*Spermatophores.*—The spermatophore of *A. talpoideum* differs most markedly from other ambystomatids by possessing a long, thin stalk of less diameter than the sperm cap, and by possessing a mid-dorsal fold running the length of the sperm cap. *A. maculatum* produces a spermatophore which may be simple, branched, or compound; one-fourth to one-half of one inch in height; and the seminal fluid may cover the supporting jelly (Bishop, 1941). The stalk is as wide as the cap. There may be 100 or more spermatophores in one group, although one male produces only 40. Wright and Allen (1909) observed 32 deposited in only 45 minutes.

The spermatophores of *A. jeffersonianum* are widely scattered according to Bishop (1941). As Bishop pictured the spermatophore, the stalk is larger than the cap and the entire structure is smaller than that of *A. maculatum.* Mohr (1931) wrote that the stalk is pyramidal.

Lantz (1930) first described the spermatophore of *A. opacum,* and it is figured by Noble and Brady (1933). It measures 4.0 to 5.5 mm in height, 6.0 mm at the base, and 2.0 mm at the apex. The summit is quadrangular or pentangular.

Details of the spermatophore of *A. tigrinum* appear to be lacking. Generally, the height is about three-fourths of an inch with a thick stalk (Stine, Fowler and Simmons, 1954).

*Oviposition.*—Oviposition resembles that of most other members of the genus *Ambystoma* where this phenomenon has been described. The description of females turning over to lay eggs resembles Hamilton's (1948) account of the egg laying *A. tigrinum nebulosum.*

Many other ambystomatids use the hind feet primarily when laying eggs on twigs. Tail waving also appears to be common in this group.

## Summary

The breeding habits of *Ambystoma talpoideum* were studied from October, 1957, until February, 1960. Mole salamanders breed in southeastern Louisiana during the winter for a period of six to fifteen days. The breeding migration is correlated with the coincidence of low temperatures and rains.

All mole salamanders collected in the breeding ponds during the breeding period were sexually mature. The mean total length of these specimens (99.5 mm) was greater than the maximum recorded total length; one specimen measured 122 mm.

Males apparently remain in the breeding pond throughout the breeding period in contrast to the females which depart from

the pond soon after oviposition; therefore, noncontinuous sampling may give an erroneous indication of the sex ratio of the breeding population.

The courtship pattern of *Ambystoma talpoideum* is most like that of its nearest relative, *Ambystoma opacum*. The courtship of the mole salamander differs from the described patterns of *A. opacum* and other species of *Ambystoma* in one or more respects.

A dorsal fold and a long, thin stalk differentiates the spermatophore of *A. talpoideum* from those of other ambystomatids. Oviposition resembles that of other species of *Ambystoma*, however. The eggs of the mole salamander have been described previously. No essential differences from the original description were found.

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Abstract

Breeding habits of a population of mole salamanders, *Ambystoma talpoideum*, were studied near Slidell, St. Tammany Parish, Louisiana. Only sexually mature individuals moved to the ponds to breed during a period of six to fifteen days during the winter. Breeding was coincident with rain and low temperatures. The courtship behavior was described and compared with that of other members of the genus. The courtship pattern was most like that of the nearest relative, *Ambystoma opacum*. The spermatophore of *A. talpoideum* is distinct.

# SALINITY RELATIONS OF SOME FISHES IN THE ARANSAS RIVER, TEXAS[1]

WILLIAM C. RENFRO,
*U.S. Bureau of Commercial Fisheries, Biological Laboratory, Galveston, Texas*

## Introduction

Fishes inhabiting bays and estuaries along the lower Gulf coast of Texas are at times subject to extremes in temperature and salinity. During droughts evaporation is high and salinity tends to increase during most months of the year. A question often discussed is: What part does salinity play in affecting distribution and abundance of fishes inhabiting this area?

Several workers have studied salinity relations of fishes in the inshore waters along the eastern and southern coasts of the United States. Hildebrand and Schroeder (1928) studied the fishes of Chesapeake Bay and included salinity records in many of their observations. Gunter (1945) published an extensive account of the distribution of the marine fishes of Texas as related to salinity. Gunter (1950) studied distribution and abundance of fishes in marginal ponds and salt flats in the Aransas National Wildlife Refuge with emphasis on changes due to temperature and salinity. The latter two studies were made during periods of normal or above normal rainfall. Simpson and Gunter (1956) described the effects of salinity on Gulf coast cyprinodonts during an extremely dry period. Simmons (1957) studied the problem in the usually hypersaline Laguna Madre of Texas.

Reid (1954) surveyed ecological relations of the fishes near Cedar Key, Florida. Reid (1955, 1956, 1957) published accounts of the changes in abundance and distribution of fishes in East Bay, Texas, before and after construction of an artificial pass connecting the blind end of that bay with the Gulf of Mexico. Kilby (1955) studied the fishes of Cedar Key and Bayport, Florida, and the extent to which salinity affected their distribution. Bailey, Winn, and Smith (1954), in their accounts of the fishes of the Escambia River, Alabama and Florida, recorded salinity relations of many marine and freshwater fishes. Because abrupt salinity stratification occurred in the Escambia River at times, Bailey *et al.* (1954) were not always able to determine the exact salinity in which some of their specimens were living. Springer and Woodburn (1960) discussed the effects of salinity, temperature, and vegetation on the distribution of fishes in the Tampa Bay area.

The objective of this study was to note the occurrence of fishes found at three stations on the Aransas River under conditions of varying salinities. The study began during September 1956 at the height of one of the worst droughts ever recorded for this section of the United States. Field work was concluded in November 1957, six months after the drought was broken by heavy rains which fell during the summer of 1957. Two aspects which previous authors have not had an opportunity to study extensively are emphasized in this paper. First, the populations sampled came from habitats in which salinity was an important variable. Secondly, variation in salinity occurring in the river provided opportunities for study of the interaction of freshwater and marine fishes.

## Description of the Area

The Aransas River has its source at approximately latitude 28° 17′N. and longitude 97° 40′ W. It terminates at Copano Bay, which is connected to the Gulf of Mexico through Aransas Bay and Aransas Pass (fig. 1). Except for drainage of water after rains there is no net seaward flow. Water stands only in the lower 28 miles of the river bed as the result of ground water addition and backup of water from the secondary bays. The river averages 100 feet in width and about 3 feet in depth although occasional deep holes may range to a depth of 15 feet.

Vegetation in the river was scanty, probably as a result of extremes in salinity. Along certain stretches of the banks were

[1] Part of a thesis presented to the Faculty of the Graduate School of the University of Texas in partial fulfillment of the requirements for the degree of Master of Arts.

found emergent plants such as sedges, water hyssops, willows, rushes, grasses, and pondweeds. Dominant algae were a blue-green alga, *Phormidium* sp., and a green alga, *Cladophora* sp. The amount of this algal vegetation increased during the latter half of 1957 with the advent of increased precipitation and lowered salinities.

Salinity of the river appeared to be controlled by: (1) precipitation, (2) evaporation, (3) intrusion of salt water from Copano Bay, (4) invasion of highly saline water from Chiltipin Creek which was polluted with brine wastes from oil fields. Salinities found at each station during the study are shown in Figure 2. Precipitation was recorded at Beeville, Texas, which lies in the middle of the watershed. Figure 2 shows that small amounts of rainfall merely dilute the saline water in the river while periods of heavy rainfall cause floods which flush it into the bays.

## Methods

Stations were sampled every 4 to 6 weeks at which time air temperature, water temperature, weather conditions, and vegetation were observed. Samples of water to be measured for salinity were taken at the surface and at a depth of 2 feet. Salinity was determined by titration with silver nitrate. Table 2 summarizes temperature - salinity conditions observed at the three stations.

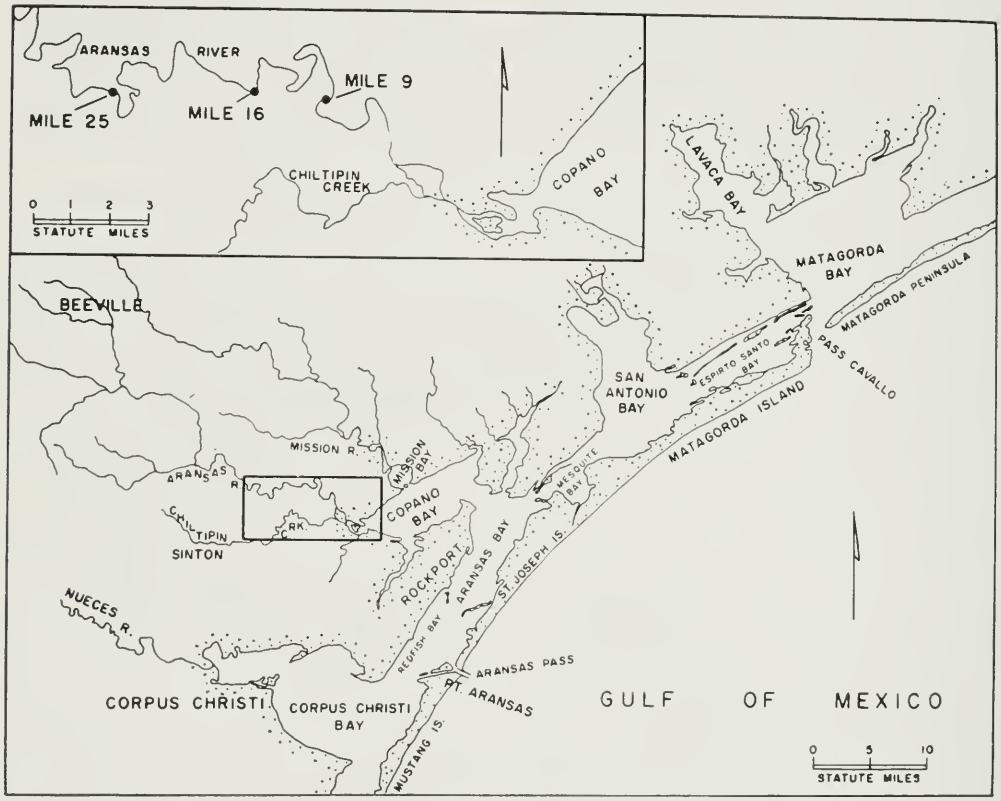


Figure 1. Central Texas coast showing location of study area.

During April, May, and June 1957 the two lower stations were not sampled due to impassable roads.

No attempt was made to sample all fish species present in the river. The data presented concern only those fishes which could be sampled within a limited area and depth along the shore. The same 30-foot bag seine was used for all collections. It was 4 feet high with wings of ⅓-inch bar mesh and bag of ¼-inch bar mesh. At each station the seine was hauled either once or twice

parallel to the shore over fixed paths and distances. All fish taken at a station were immediately preserved in 10 percent formalin for subsequent examination. All measurements are standard lengths to the nearest millimeter. Table 1 summarizes the distribution by salinity of the fishes collected.

Stations at 9, 16, and 25 miles from the mouth of the river being most accessible were selected as collection sites (fig. 1). Mile 9 and Mile 25 had gently sloping bottoms. At Mile 16 the bottom sloped gently for about 8 feet, then more abruptly so that at a distance of 12 feet offshore the depth had increased to 6 feet. The bottom at all three stations consisted of silt and mud.

## Salinities Recorded for Species Observed

*Lepisosteus spatula* Lacépède, Alligator gar—Only three alligator gars were taken with the type of gear used although the

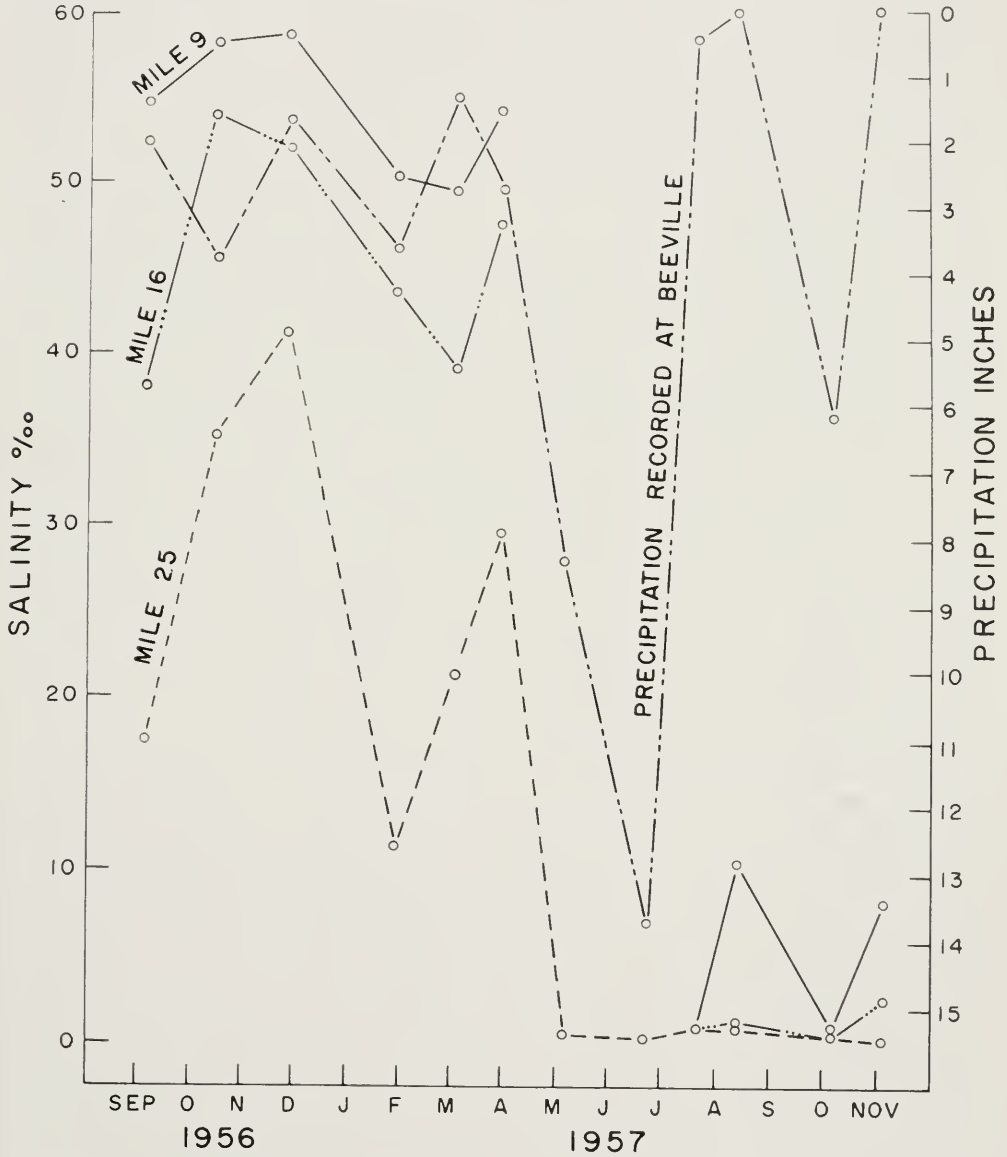


Figure 2. Salinity regimes—Aransas River. Precipitation at Beeville, Texas is the cumulative total recorded between collections.

species was abundant in the river at all times. One specimen approximately 1 meter long was captured at Mile 25 in October 1956 in a salinity of 35.2‰. Another was taken in October 1957 at Mile 25 in a salinity of 0.05‰. It measured 425 mm in length. The third was a small specimen 70 mm long collected in November 1957 in a salinity of 8.3‰ at Mile 9. Gars were observed in the river during every month of the year and in every salinity (0.05 to 58.6‰).

*Brevoortia patronus* Goode, Largescale menhaden.—One specimen 120 mm long was collected at Mile 9 in March 1957 in a salinity of 54.3‰. At the same time at Mile 16 another specimen measuring 32 mm was taken in 47.6‰. In July 1957 three individuals, 52, 61, and 64 mm long were found at Mile 16 in 0.5‰.

*Dorosoma cepedianum* (LeSueur), Gizzard shad.—Sixty specimens were collected in salinities ranging from 0.05‰ to 41.3‰. No juvenile fish were taken in the first half of the study when the river was highly saline. Forty specimens less than 40 mm long were caught in July 1957 in salinities of 1.1‰ or less. No small individuals were taken in salinities above 1.1‰. This supports the conclusions of Gunter (1945) that the gizzard shad inhabiting coastal waters must return to fresh water to spawn. Only two adult gizzard shad were taken in highly saline water; one measuring 114 mm was caught in 35.2‰ and the other, 104 mm in length, was taken in 41.3‰.

*Dorosoma petenense* (Günther), Threadfin shad.—Thirty-three juveniles were collected. One specimen 35 mm in length was caught in a salinity of 10.4‰ at Mile 9 during August 1957. All others measured less than 60 mm in length and were taken in salinities of 1.0‰ or lower, indicating that this species also might require fresh water to spawn.

*Anchoa mitchilli* (Valenciennes), Bay anchovy.—A total of 228 individuals of this species was taken. They ranged from 23 to 57 mm in length although most were between 40 and 50 mm. Bay anchovies were found in salinities from 0.05‰ to 8.3‰ and none were taken during 1956 when the river was hypersaline.

*Notropis lutrensis* (Baird and Girard), Red shiner.—Three juveniles were collected in August 1957 in a salinity of 1.0‰.

TABLE 1.
*Occurrence by salinity of fishes collected.*

| Salinity ‰ | from: .05 to: 1.0 | 1.1 5.0 | 5.1 15.0 | 15.1 25.0 | 25.1 35.0 | 35.1 45.0 | 45.1 55.0 | 55.1 58.6 |
|---|---|---|---|---|---|---|---|---|
| Collections in this salinity range | 10 | 2 | 3 | 2 | 1 | 5 | 7 | 2 |
| *Lepisosteus spatula* | 1 | — | 1 | — | — | 1 | — | — |
| *Brevoortia patronus* | 3 | — | — | — | — | — | 2 | — |
| *Dorosoma cepedianum* | 47 | 5 | 6 | — | — | 2 | — | — |
| *Dorosoma petenense* | 32 | — | 1 | — | — | — | — | — |
| *Anchoa mitchilli* | 114 | 79 | 35 | — | — | — | — | — |
| *Notropis lutrensis* | 3 | — | — | — | — | — | — | — |
| *Ictalurus furcatus* | 1 | — | 1 | — | — | — | — | — |
| *Syngnathus scovelli* | 1 | — | — | 143 | — | 21 | — | — |
| *Fundulus grandis* | 8 | — | 11 | 2 | — | 4 | 17 | 2 |
| *Lucania parva* | 45 | — | — | 3 | 6 | 19 | 1 | — |
| *Cyprinodon variegatus* | 144 | 12 | 46 | 28 | 11 | 173 | 161 | 13 |
| *Gambusia affinis* | 22 | 6 | 1 | 4 | — | — | — | — |
| *Mollienisia latipinna* | 13 | — | 2 | 61 | 1 | 129 | 1 | — |
| *Menidia beryllina* | 285 | 124 | 75 | 302 | 484 | 137 | 77 | 7 |
| *Mugil cephalus* | 10 | 1 | 18 | 57 | 9 | 30 | 31 | 4 |
| *Mugil curema* | 1 | — | — | — | — | — | — | — |
| *Micropterus salmoides* | — | — | — | 1 | — | — | — | — |
| *Chaenobryttus gulosus* | — | — | — | 2 | — | — | — | — |
| *Lepomis macrochirus* | 41 | 8 | — | 6 | — | — | — | — |
| *Lepomis megalotis* | 4 | — | — | — | — | — | — | — |
| *Bairdiella chrysura* | — | 2 | — | — | — | — | — | — |
| *Encinostomus argenteus* | — | — | 3 | — | — | — | — | — |
| *Cichlasoma cyanoguttatum* | 7 | 1 | — | 4 | — | — | — | — |
| *Dormitator maculatus* | — | — | — | — | — | — | 1 | — |
| *Gobiosoma bosci* | 1 | — | — | 4 | — | — | — | — |
| *Trinectes maculatus* | 1 | 1 | 1 | — | — | — | — | — |

*Ictalurus furcatus* (LeSueur), Blue catfish.—Two specimens of this fresh-water catfish were taken. One measured 104 mm and was found at Mile 16 in a salinity of 1.0‰. The second, measuring 85 mm in length, was caught in a salinity of 10.4‰ at Mile 9. Gunter (1945) found a few blue catfish in salinities up to 6.9‰ in Copano Bay.

*Syngnathus scovelli* (Evermann and Kendall), Gulf pipefish.—In September 1956, 164 specimens were collected from two stations. Twenty-one came from a salinity of 38.1‰ at Mile 16 and 143 were found in a salinity of 17.4‰ at Mile 25. Nearly all the males were either carrying developing eggs and embryos or had recently delivered broods (as indicated by their enlarged, flaccid pouches). One other pipefish, a ripe female measuring 89 mm, was taken in a salinity of 0.06‰ during June 1957.

Pipefish are usually found in or near submerged vegetation, and salinity might well affect their distribution and abundance by altering the amount of vegetation available to them. Simmons (1957) found this species abundant in vegetation in salinities to 45‰.

*Fundulus grandis* Baird and Girard, Gulf killifish.—Forty-four Gulf killifish ranging in length from 21 to 90 mm were taken in salinities of 0.05 to 58.6‰. Table 2 shows that this species occurred throughout a wide range of salinity-temperature combinations. Small and large killifish were found together in both fresh and hypersaline water. Simpson and Gunter (1956) took *F. grandis* in salinities varying between 1.8‰ and 76.1‰.

*Lucania parva* (Baird and Girard), Rainwater killifish.—Seventy-four specimens ranging in length from 9 to 32 mm were collected in salinities from 0.05‰ to 47.6‰. Sixteen were taken at one station in a salinity of 38.1‰, and only four were caught in salinities above this. Over 60 percent were found in salinities less than 10.0‰.

Gunter (1945) found this species most abundant in salinities between 10.0‰ and 15.0‰. Kilby (1955) took 81 percent of his specimens from waters of 10‰ or less. Simpson and Gunter (1956) found 39.4 percent of the rainwater fish they collected in salinities below 10.0‰, the greater proportion having been taken at salinities between 18.4‰ and 48.2‰. In Florida, Springer and Woodburn (1960) found this species to be most common in salinities greater than 25‰. They stated that vegetation rather than salinity is probably the most important factor affecting its distribution.

*Cyprinodon variegatus* Lacépède, Sheepshead minnow.—A total of 588 sheepshead minnows was collected, accounting for 18.5 percent of all fishes taken. They were found in salinities ranging from 0.05‰ to 58.6‰.

Simpson and Gunter (1956) caught 2,009 *C. variegatus* in a salinity of 142.4‰ and stated that, so far as they knew, "this was the highest salinity at which living fishes have been reported." During August 1957 the writer kept one specimen in a small aquarium for 7 days in a salinity of 125.2‰ and when the salinity was raised to 145.6‰ by the addition of sea-salt crystals, it lived an additional 37 hours. However, as Simpson and Gunter *(op cit)* emphasize, "water at such salinity is not sea water for some salts are precipitated before sea water attains such concentration and the salt complex is changed."

In December 1957 a pair of *C. variegatus* kept in an aquarium in the laboratory spawned four eggs. These eggs were transferred to a shallow glass dish 100 mm in diameter and filled with sea water to a depth of 25 mm. The dish was placed in a water-filled pan to avoid rapid changes in temperature and the eggs were observed daily. On the afternoon of the 12th day the eggs had not hatched, but on the morning of the 14th day three larval fishes were found darting rapidly around the dish. They measured 4 mm in standard length and had absorbed their yolk sacs. Evaporation had decreased the depth of the water in the dish to 8 mm and salinity was in excess of 110‰. Temperature during incubation ranged from 17.4° C to 27.5°C. Within the ranges recorded, increasing salinity and changes in temperature did not inhibit incubation of the eggs and young were able to survive in hypersaline water.

There appears to be no correlation between size and salinity as small and large specimens were found in all salinities encountered. Radical changes in abundance were not noted even during periods of extremes in salinity and temperature (Table 2).

TABLE 2.

*Salinity-temperature conditions at three stations on the Aransas River and the number of individuals of several species taken therein.*

| Date | Station | Salinity ‰ | Water temperature °C | *Fundulus grandis* | *Lucania parva* | *Cyprinodon variegatus* | *Mollienisia latipinna* | *Menidia beryllina* | *Mugil cephalus* |
|---|---|---|---|---|---|---|---|---|---|
| | 9 | 54.9 | 29.3 | 1 | — | 6 | — | — | 2 |
| 9/ 4/56 | 16 | 38.1 | 27.9 | 3 | 16 | 90 | 95 | 76 | 8 |
| | 25 | 17.4 | 29.8 | — | 2 | 7 | 59 | 148 | 2 |
| | 9 | 58.2 | 29.5 | — | — | — | — | 1 | 4 |
| 10/14/56 | 16 | 54.0 | 28.0 | — | — | 3 | — | 2 | — |
| | 25 | 35.2 | 29.6 | — | — | — | — | — | 4 |
| | 9 | 58.6 | 16.0 | 2 | — | 13 | — | 6 | — |
| 11/25/56 | 16 | 52.2 | 16.0 | — | — | 8 | 1 | 31 | — |
| | 25 | 41.3 | 18.6 | — | 3 | 4 | 34 | 51 | — |
| | 9 | 50.3 | 16.0 | 3 | — | 52 | — | 6 | 1 |
| 1/30/57 | 16 | 43.9 | 20.5 | — | — | 62 | — | 1 | 2 |
| | 25 | 11.4 | 18.9 | 1 | — | 3 | — | 58 | 17 |
| | 9 | 49.5 | 21.0 | 3 | — | 15 | — | 7 | 8 |
| 3/ 2/57 | 16 | 39.0 | 21.2 | 1 | — | 17 | — | 9 | 16 |
| | 25 | 21.0 | 21.0 | 2 | 1 | 21 | 2 | 157 | 55 |
| | 9 | 54.3 | 21.2 | 10 | — | 30 | — | 20 | 9 |
| 3/30/57 | 16 | 47.6 | 21.2 | — | 2 | 47 | — | 11 | 11 |
| | 25 | 29.5 | 21.2 | — | 6 | 11 | 1 | 481 | 9 |
| 5/ 5/57 | 25 | 0.08 | 24.2 | — | — | 7 | 11 | 2 | 10 |
| 6/22/57 | 25 | 0.06 | 26.2 | — | 4 | — | — | 1 | — |
| | 9 | 0.7 | — | 5 | — | 90 | — | — | — |
| 7/20/57 | 16 | 0.5 | — | — | — | 4 | — | — | — |
| | 25 | 1.1 | 34.5 | — | — | — | — | 101 | 1 |
| | 9 | 10.4 | 32.9 | 6 | — | 21 | — | — | 1 |
| 8/14/57 | 16 | 1.0 | 31.2 | — | — | 7 | — | 5 | — |
| | 25 | 1.0 | 31.2 | — | 2 | 2 | 2 | 98 | — |
| | 9 | 0.8 | 27.2 | 1 | — | 12 | — | 13 | — |
| 10/ 5/57 | 16 | 0.06 | 27.0 | — | — | 5 | — | 6 | — |
| | 25 | 0.05 | 29.0 | 2 | 1 | — | — | 2 | — |
| | 9 | 8.3 | 24.6 | 4 | — | 22 | 2 | 17 | — |
| 11/ 2/57 | 16 | 2.7 | 24.5 | — | — | 12 | — | 23 | — |
| | 25 | 0.2 | 24.2 | — | 38 | 17 | — | 158 | — |

*Gambusia affinis* (Baird and Girard), Mosquitofish.—Thirty-three specimens from 9 to 36 mm long were collected. All but five were taken in salinities of 1.1‰ or less. In September 1946 four specimens were found in a salinity of 17.4‰. During November 1957 one mosquitofish measuring 19 mm was found in a salinity of 8.3‰ at Mile 9.

Simpson and Gunter (1956) caught one *G. affinis* in a salinity of 20.6‰. Kilby (1955) stated: "... it thus appears that the fish is most numerous in protected waters such as shallow pools and vegetated areas where the salinities are lowest, at least periodically, but it can tolerate salinities up to at least 26‰."

*Mollienisia latipinna* LeSueur, Sailfin molly.—Two hundred and seven individuals ranging between 12 and 44 mm in length were caught in salinities of 0.08‰ to 52.2‰. This species is ordinarily found in schools and thus capture is, for the most part, fortuitous. In fact, three seine hauls accounted for more than 90 percent of the specimens collected.

Herre (1929) noted the remarkable salinity tolerance of *M. latipinna* in populations which had been transported from the United States via the Hawaiian Islands and accidentally naturalized in the Philippine Islands. He found the species to be abundant in salinities from 32‰ to 87‰, and that the latter salinity appeared to be near

its limit of toleration, for in ponds with a salinity of 94‰, it had entirely disappeared.

*Menidia beryllina* (Cope), Tidewater silverside.—A total of 1,491 individuals was collected. The tidewater silverside is probably the most abundant species in the area sampled. They were found in salinities from 0.05‰ to 58.6‰ and in widely differing combinations of salinity and temperature. Collections taken over a wide range of salinities had both small and large specimens in fairly constant ratios. Gunter (1945) found specimens of *M. beryllina* to be slightly larger in waters above 25‰ than in those below that salinity.

*Mugil cephalus* Linnaeus, Striped mullet.—One hundred and sixty striped mullets were collected during this study. Adult mullets easily escaped the collecting gear used, and only six specimens captured were more than 100 mm long. The great majority were juveniles measuring 22 to 42 mm taken from March to May 1957. Juveniles were found in salinities ranging from 0.08‰ to 54.3‰. Larger mullets were observed jumping in the river during every month and in every salinity encountered. Mullets at all ages are euryhaline.

Since it is difficult to separate immature *M. cephalus* and *M. curema*, it is possible that some of the smaller specimens were *M. curema*.

*Mugil curema* Valenciennes, White mullet.—One white mullet measuring 79 mm was taken at Mile 25 in a salinity of 0.2‰. Its fins were heavily infested with leeches.

*Micropterus salmoides* (Lacépède), Largemouth bass.—At Mile 25 on September 4, 1956 a largemouth bass 151 mm long was caught in a salinity of 17.4‰. Two other species of the family Centrarchidae and one cichlid species were included in this unusual collection. It is unfortunate that further salinity determinations for the upper reaches of the river were not made on this date to determine the salinities these typically fresh-water species passed through to reach this station. Hildebrand and Schroeder (1928) reported *M. salmoides* from a salinity of 12.87‰ taken at Lewisetta, Virginia, in August 1921. Of the 18 specimens reported in Kilby's (1955) collections, only 1 was taken where the salinity reached 11.8‰. Renfro (1959) concluded that salinities above 9‰ were progressively more critical, but that this species might be expected to survive several weeks in lower salinities.

Chipman (1959) studied fishes in a Louisiana pond which was polluted with oil well brine wastes. He noted mortalities of fresh-water species which died during a 7-day period in which salinity was first recorded at 16.5‰, rose to 20.9‰ on the 5th day, declined to 5.8‰ and 6.6‰ respectively on the 6th and 7th days. He found one largemouth bass dead in a salinity of 20.6‰.

*Chaenobryttus gulosus* (Cuvier), Warmouth.—Two specimens measuring 68 and 72 mm taken in the collection mentioned above (salinity 17.4‰) were the only two warmouths observed.

During his 7-day study Chipman (1959) found 748 warmouths dead. He found in laboratory toxicity experiments that 12 specimens tested died in salinities between 10.7‰ and 16.9‰.

*Lepomis macrochirus* Rafinesque, Bluegill.—Six subadults were taken at Mile 25 September 4, 1956 in 17.4‰. On November 2, 1957 six young specimens 28 to 35 mm in length were collected at Mile 16 in 2.7‰. The remaining 43 bluegills taken were found in salinities of 1.1‰ or less and ranged in length from 16 to 83 mm. Chipman (1959) noted 523 dead bluegills during his 7-day study.

*Lepomis megalotis* (Rafinesque), Longear sunfish.—Four subadults were taken in collections during the latter half of 1957. All were caught in salinities of 0.2‰ or less.

*Bairdiella chrysura* (Lacépède), Silver perch.—Two specimens measuring 86 and 93 mm were taken on November 2, 1957 in a salinity of 2.7‰. Gunter (1945) found this species to be more or less indifferent to salinity. Kilby (1955) caught silver perch in salinities from 5.6‰ to 27.3‰. Springer and Woodburn (1960) took this species in salinities from 3.7‰ to 35.0‰ with most being captured in salinities above 20.0‰.

*Eucinostomus argenteus* Baird and Girard, Spotfin mojarra.—Three young individuals 40, 41, and 43 mm long were caught at Mile 9 in a salinity of 8.3‰. Species identification of this difficult genus is provisional.

*Cichlasoma cyanoguttatum* (Baird and Girard), Rio Grande perch.—Twelve Rio Grande perch were taken during the study,

four being found in the collection of September 4, 1956 at Mile 25 in 17.4‰. The remaining specimens were taken at various times in salinities of 1.1‰ or less.

*Dormitator maculatus* (Bloch), Fat sleeper.—One specimen 38 mm long was caught on September 5, 1956 at Mile 9 in a salinity of 54.9‰. As this species is known to penetrate far inland (Moore 1957) it appears to be tolerant to a wide range of salinities.

*Gobiosoma bosci* (Lacépède), Naked goby.—Five specimens were collected, three being taken in 21.1‰, one in 17.4‰, and one in a salinity of 0.2‰.

*Trinectes maculatus* (Bloch and Schneider), Hogchoker. — Three hogchokers were taken in salinities of 0.8‰, 2.7‰, and 8.3‰. Simmons (1957) stated that the hogchoker was common in salinities of 50‰ or less during the fall months in the Laguna Madre.

## Discussion and Summary

During this study salinity in the river varied over a broad range and fluctuations were sometimes rapid. Water levels were constant except during floods; water temperatures observed varied from 16.0° C to 34.5° C, and the shore and bottom configuration was stable. Most of the species taken were those which are characteristically found along the shoreline, and it must be emphasized that the conclusions reached do not extend to the fishes which were undoubtedly present in the river but which were not taken with the gear used.

As previously stated, the objective of the study was to note the occurrence of fishes in varying salinities. It is felt that the data obtained allow inferences concerning salinity tolerances. Salinity tolerance as here used is construed to be the capacity of a fish to endure specific levels of dissolved salts. The writer is aware that the relationship of a fish to its environment is a complex phenomenon. A fish is obliged to adjust not only to changing salinity, but to changes in temperature, dissolved oxygen concentration, food supply, and numerous other interrelated parameters of its environment. In the case of critical salinities (those concentrations of dissolved salts too low or high for the fish to withstand indefinitely) we might expect exposure time to become a factor. That is, in increasingly more critical salinities, the fish's survival time must decrease. For this reason, it is possible that some of the fishes taken were transients, being found in salinities higher or lower than they could withstand for more than limited intervals.

Twenty-six species belonging to 8 orders and 16 families were collected. Nine species (*Dorosoma petenense, Notropis lutrensis, Ictalurus furcatus, Gambusia affinis, Micropterus salmoides, Chaenobryttus gulosus, Lepomis megalotis, Lepomis macrochirus,* and *Cichlasoma cyanoguttatum*) are fresh-water fishes, i.e., they are found in fresh water and occur in salt waters only occasionally or in reduced numbers. Five of these species were found in a salinity of 17.4‰, which indicates that they have at least temporary tolerance to this salinity.

Why then do not these fresh-water fishes occur in greater numbers when the salinity in the river has been decreased to a level which they are known to tolerate? Probably they do not because of the innate characteristics of this particular hydrographic system. When salinity is lowered these fishes venture into the lower reaches of the river. Before their numbers can reach significant proportions, however, the salinity begins to increase and they are either forced back upstream or perish. Population densities of these "fresh-water" species appear to vary inversely with salinity.

The gar, *Lepisosteus spatula,* and the clupeid, *Dorosoma cepedianum,* were tolerant of all salinities observed and might well be considered euryhaline. Presumably spawning must take place in fresh water.

Eight species (*Brevoortia patronus, Anchoa mitchilli, Syngnathus scovelli, Bairdiella chrysura, Eucinostomus argenteus, Gobiosoma bosci, Trinectes maculatus,* and *Mugil curema*) are commonly found during part or all of their lives in salinities between fresh water and sea water. With the exception of the goby, all enter the Gulf at times. However, these species are probably not well adapted for life in salinities above 35‰.

The remaining seven species (*Fundulus grandis, Lucania parva, Cyprinodon variegatus, Mollienisia latipinna, Menidia beryllina, Mugil cephalus,* and *Dormitator maculatus*) are particularly fitted for life in a wide range of salinities. They are able to maintain their populations in the river regardless of changes in salinity. Most of these species

were represented in collections in which salinity and temperature were at extreme levels. They are among the hardiest of the smaller fishes found along the coast of the Gulf of Mexico. These are the fishes found most often and in greatest aboundance along the shorelines of inside waters of the northwestern Gulf of Mexico.

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## Abstract

Fishes were collected at three stations on the Aransas River, a nonflowing, normally brackish body of water on the Central Texas Gulf Coast. A drought prevailing during the first half of the study produced a highly saline environment. Subsequent rainfall and lowered salinities provided an opportunity to note the occurrence of fishes taken at three stations over a wide range of salinities. Twenty-six species are categorized as to their salinity tolerance. Five species of freshwater fishes were found in a salinity of 17‰. Seven species were found to tolerate salinities ranging from nearly fresh to well above 45‰.

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# ECOLOGY OF THE RICE RAT, *ORYZOMYS PALUSTRIS* (HARLAN), ON BRETON ISLAND, GULF OF MEXICO, WITH A CRITIQUE OF THE SOCIAL STRESS THEORY

NORMAN C. NEGUS,
EDWIN GOULD,
and
ROBERT K. CHIPMAN,

*DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY,*
*NEW ORLEANS, LOUISIANA*

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NORMAN C. NEGUS,
EDWIN GOULD,
and
ROBERT K. CHIPMAN,

*Department of Zoology, Tulane University, New Orleans, Louisiana*

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## I. Introduction

An investigation of rice rat (*Oryzomys palustris*) populations on Breton Island, Louisiana, was initiated in July, 1957. Results contained in this report are based on data accumulated during a three-year period of this continuing project.

The advantages of this island population for study are several: (1) Breton Island constitutes a large unit of undisturbed habitat; (2) the rice rat is present in substantial numbers and is the only small rodent species on the island, thus constituting one of the simplest natural small mammal communities on which to conduct studies; and (3) the insular location precludes the possibility of appreciable immigration and emigration of animals.

As is typical of most southern mammals, relatively little intensive study has been made of the biology of *Oryzomys*. Hamilton (1946) described the habits of rice rats in Virginia and the development of young in captivity to an age of 21 days. Conaway (1954) studied the estrous cycle and contributed further information on the development of young. He found the age of puberty to be 42 days in males and 57 days in females. Goodpaster and Hoffmeister (1952), Svihla (1931), Harris (1953), and others described various aspects of the habits and inter-specific relationships of *Oryzomys*. Gilmore (1947) reported on the "cyclic" behavior of rata-muca (*Oryzomys xanthaeolus*) populations in Peru.

There is a dearth of information regarding home ranges and population densities in any of the diverse habitats in which the genus occurs. *Oryzomys* has rather wide ecological amplitude in North America as evidenced by its occurrence in a variety of habitats, including coastal and freshwater marshes, oldfields, bottomland forests, pinelands, mixed forest types, and even the high mountains of South Carolina (Coleman, 1948). Historically, *Oryzomys* had a wider distribution in North America than at present. Gilmore (1946) found remains of rice rats in a prehistoric Indian site in the rugged terrain of the Allegheny Plateau of southwestern Pennsylvania.

*Oryzomys* eats seeds and herbaceous plant parts as well as insects and other animal matter. A nine-month to year-round breeding season has been attributed to the rice rat (Brimley, 1923; Goldman, 1918; Svihla, 1931).

## II. Description of Breton Island

Breton Island is located about 10 miles east of the Mississippi River Delta at 29°28′ North Latitude. The island is divided into two islets, North and South Breton, by a channel about 400 yards wide. South Breton, the main study site, is three miles long by about one-half mile at its greatest width (fig. 1).

Breton Island is rapidly being eroded. Wind and wave action have reduced its size from eleven to five miles in length since Lockett's description in 1870 (Russell, 1936). Driftwood littered the beaches in recent years and, according to Russell's account, contributed to the great density of snakes. Human families inhabited the island prior to the 1915 hurricane, though signs of their occupancy have since vanished.

A common misconception of southern regions is that of a changeless climate. On an island such as Breton, striking climatic extremes occur seasonally. In midsummer the intense sunlight creates a scorching environment at the surface of the sand during the day. As the season progresses, squalls and even hurricanes cause heavy wave action, often flooding the sedge areas.

Frequent cold fronts, accompanying the arrival of winter, may cause the temperature to drop 20+°F within a few hours. During this season rice rats may be subjected to temperatures varying from freezing to 70°F in an interval of several days. In spring, when the vegetation begins to grow, the rats have a new food supply at a crucial time when breeding may begin, continue, or even stop.

Marked vegetational zonation is present on South Breton Island. We have divided the island into five areas based on the vegetation and the elevation of the land. The southern margin of the island is an area of bare sandy beach varying in width from a few feet to 200 feet. The beach area is usually two to three feet above mean sea level and virtually devoid of vegetation. Inland, the ground approaches sea level and the soil becomes more silty. This area supports a broad strip of sedges and grasses dominated by *Fimbristylis castanea* with several associated shrubs such as groundsel bush

Figure 1. Aerial photograph of South Breton Island, showing location of operations shack (A) and quadrat L-1 (B). Note para lel zonation of vegetation. South shore is on the right in the photograph.

(*Baccharis halimifolia*) and rattlebox (*Daubentonia drummondii*). This sedge association is confined to the western half of the island (fig. 2).

North of the sedge association is a stationary sand dune area, located parallel to the south shore. These dunes separate the sedge from a wax myrtle (*Myrica cerifera*) association on the western half of the island. The sand dunes are highest at the eastern half of the island where they may be 15 feet. The height of the sand dunes decreases progressively toward the western end of the island, where they are virtually absent.

The higher and rather level ground supports a dense stand of *Yucca* and *Opuntia* along portions of the sand dunes farthest from the beach. An impenetrable stand of wax myrtle dominates a considerable portion of the interior north of the sand dunes. This association inhabits somewhat higher ground than the sedge association (fig. 3).

A zone of honey mangrove (*Avicennia nitida*) extends north of the wax myrtle stand, particularly in low swampy areas and along the relatively sheltered irregular north shore. The substrate is heavily silted. Both the mangrove and wax myrtle associations

Figure 2. *Fimbristylis* community near east end of quadrat L-1. Photograph taken in June, 1960. Shrubby vegetation is *Baccharis halimifolia* (groundselbush). Rice rats were most abundant in this habitat.

Figure 3. *Opuntia-Yucca* community on high ground of interior on South Breton Island.

are dissected by a network of brackish water channels and lagoons.

The zones of vegetation are represented by the following species. The less common plants are not listed. Scientific names are according to Small (1933).

Beach: *Cakile edentula* (Bigel.) Hook., *Daubentonia drummondii* Rydb.

Sedge association (livetrap study area): *Spartina patens* (Ait.) Muhl., *Uniola paniculata* L., *Cyperus paniculatus* Rottb., *Eleocharis caribaea* (Rottb.), *Fimbristylis castanea* (Michx.) Vahl., *Juncus validus* Coville, *Rumex persicarioides* L., *Lepidium virginicum* L., *Croton punctatus* Jacq., *Sabatia stellaris* Pursh, *Heliotropium curassavicum* L.

Stationary sand dunes: *Hydrocotyl umbrellata* L., *Ipomoea angustifolia* Jacq.

Wax myrtle association: *Myrica cerifera* L., *Baccharis halimifolia* (L.) DC.

Honey mangrove association: *Salicornia* sp., *Batis maritima* L., *Avicennia nitida* Jacq., *Borrichia frutescens* (L.) DC.

Prickly pear association: *Yucca gloriosa* (*teste* Lloyd and Tracy 1901), *Smilax* sp., *Rubus trivialis* Michx., *Opuntia humifusa* Raf. (*teste* Lloyd and Tracy, 1901, as *"O. opuntia"*), *Erechtites hieracifolia* (L.) Raf.

With the exception of birds, the terrestrial vertebrate fauna is limited. Scientific and common names of the species recorded are taken from the following checklists: Schmidt (1953)—reptiles; AOU (1957)—birds; Hall and Kelson (1959)—mammals. The known reptilian fauna includes the following, none of which is common except *Lygosoma:* diamond-back terrapin (*Malaclemys terrapin* Schoepff), sea turtle (*Lepidochelys olivacea* Garman) found dead on the beach, alligator (*Alligator mississippiensis* Daudin), lizards (*Anolis carolinensis* Voigt, and *Lygosoma laterale* Say), water snake (*Natrix sipedon clarki* Baird and Girard), spotted king snake (*Lampropeltis getulus holbrooki* Stegner), cottonmouth moccasin (*Ancistrodon piscivorus* Lacépède).

No amphibians are known to occur on the island. The following mammals are known to exist on the island: swamp rabbit (*Sylvilagus aquaticus* Bachman), rice rat (*Oryzomys palustris* (Harlan)), muskrat (*Ondatra zibethicus* L.), nutria (*Myocaster copyus* E. Geoffroy St.-Hilaire), raccoon (*Procyon lotor* L.), otter (*Lutra canadensis* Schreber).

A great variety of birds inhabits the island communities. The species composition and numbers of birds vary considerably throughout the seasons. The following species are known to nest on the island: brown pelican (*Pelecanus occidentalis* L.), snowy egret (*Leucophoyx thula* (Molina)), Louisiana heron (*Hydranassa tricolor* (Müller)), black duck (*Anas rubripes* Brewster), clapper rail (*Rallus longirostris* Boddaert), willet (*Catoptrophorus semipalmatus* (Gmelin)), black skimmer (*Rynchops nigra* L.), yellow-billed cuckoo (*Coccyzus americanus* (L.)), common nighthawk (*Chordeiles minor* (Forster)), yellowthroat (*Geothlypis trichas* (L.)), red-winged blackbird (*Agelaius phoeniceus* (L.)), boat-tailed grackle (*Cassidix mexicanus* (Gmelin)), orchard oriole (*Icterus spurius* (L.)).

Several barn owls (*Tyto alba* Bonaparte) were observed during the winter of 1957. Their pellets were, for the most part, composed of rice rat remains. Several pigeon hawks observed throughout their nesting season may be another predator of the rice rats. A single marsh hawk (*Circus cyaneus* L.) was also recorded.

## III. Materials and Methods

### A. *Study Areas*

Study areas were located in the sedge community where rice rats were more abundant than in other habitats. Within this community two livetrap quadrats were located where the ground was quite level and the vegetation was the same over the whole plot. The quadrats were located along the south side of the island about 150 feet from the shore line, as indicated in the aerial photograph (fig. 1). Painted stakes driven into the ground 50 feet apart marked the location of trapsites. One unit (live quadrat L-1) measured 800 x 400 feet (7.3 acres) and the other (live quadrat L-3) 500 x 200 feet (2.2 acres).

### B. *Field Techniques*

Animals in quadrats L-1 and L-3 were captured with large, collapsible Sherman live traps, set out for two to five nights in succession. Traps were checked early in the morning. Initially the traps were baited with rolled oats, but this was discontinued as baiting made no difference in the catch. The animals were taken to our cabin (in center of the island, (fig. 1), and examined. Each animal, after being placed in a plastic bag and anesthetized with ether, was weighed and its reproductive status, age, and pelage condition tabulated. Criteria used in evaluating reproductive condition of females were: open or closed vaginal orifice, teat size, development of mammary tissue,

and presence and size of embryos as determined by palpation. The size and position of testes (inguinal, scrotal, or abdominal) were used to assess reproductive status of males. The animals were finally toe-clipped for future identification. Later in the investigation, the standard total length, in millimeters, was also taken. After the animals were examined and toe-clipped, they were returned to the trapsite from which they had come. Animals were generally returned to the field before noon.

Dead samples were initially collected by setting Victor mousetraps and Museum Specials baited with oat meal every 30 feet in the sedge community. Later, Sherman live traps were used. Dense wax myrtle stands were also trapped but yielded very small samples. The animals were fixed in formalin and later preserved in alcohol after removal of adrenal glands, bacula, stomachs and reproductive tracts of females.

### C. *Laboratory Techniques*

Considerable and varied data were recorded from samples of animals sacrificed for laboratory examination. Stomachs were emptied of their contents. The identity of contents was determined insofar as possible as well as occurrence, frequency and per cent of volume. The major portion of the stomach contents was too well masticated for specific identification. However, when animal and plant material were well preserved, the parts were separated and identified. No attempt was made to distinguish the various seed species, though stomach contents were saved for further analysis.

The adrenals were removed and placed under a binocular microscope to facilitate the careful and complete removal of fat and connective tissue. Right and left adrenals were kept separate and later weighed on an analytical chainomatic balance to the nearest 0.1 milligram. Each adrenal was first dried by lightly rolling it over several times on absorbent filter paper before being weighed in an air-tight weighing jar.

The female reproductive tracts, tagged on the right uterine horn, were fixed in F.A.A., while some were fixed in formalin. The ovaries were removed, imbedded in tissuemat, sectioned, mounted, and stained with Delafield's or Harris' hematoxylin and eosin and subsequently examined to determine ovarian activity and reproductive history. The number and crown-rump measurements of embryos in pregnant females were recorded, and placental scar counts were made in post-partum specimens.

Weight, total length, pelage condition, and degree of ossification of the distal epiphyses of the radius and ulna were used as criteria for age determination. A Japanese Softex X-ray Unit (Koizumi X-ray Products Co., Tokyo) was used to examine the extent of ossification of the distal epiphyses of the radius and ulna in known-age and dead sample animals to separate sub-adults from adults. The pelage of all animals was examined and flat skins of selected pelage stages were prepared.

Litters of known ages were obtained from pregnant females taken from the field in addition to females mated in the laboratory. These animals of known ages were sacrificed at various time intervals. At 7 to 14 day intervals the animals were weighed, measured and examined for reproductive activity and pelage condition.

## IV. Results

### A. *Home Range and Movements*

The initial size of each of two live trapping quadrats was 200 x 500 feet. One of these was later expanded to 800 x 400 feet. A trap interval of 50 feet was selected on the basis of known home ranges of other small mammals( Fitch, 1958; Stickel, 1948). Home range data were obtained for marked animals by recaptures over a period of several months. The same quadrats were trapped each time at one or two month intervals. Over a period of 33 months, 174 animals were recaptured from one to nine times each. No attempt was made to recognize home range of any animal captured less than three times. A total of 53 rats were captured three to nine times each ($\bar{x} = 4$), allowing us to make an estimate of home range. Home ranges were estimated by Blair's (1940) technique (inclusive boundary zone) of connecting recapture sites. The mean home range area for males, based on 23 individuals is 0.81 acres (range: 0.23-2.26 acres). The mean home range area for 12 females is 0.51 acres (range: 0.23-1.13 acres). There is a tendency for home ranges to be oriented with their long axes roughly parallel to the shoreline, probably a natural

consequence of the parallel zonation of the sedge community.

The stability of adult *Oryzomys* home ranges on Breton Island is noteworthy. For example, eight animals that were classed as adults when originally marked remained in their same home ranges over periods varying from four to seven months ($\bar{x} = 5.5$ months). One adult male was recaptured three times over a period of four months. He was finally recaptured again in the same home range 20 months after the original capture!

Considerable overlap of home ranges was recorded. Further, general instability of home ranges among young individuals was indicated by frequent recaptures at widely scattered locations. The greatest recorded movement is that of two old adult males, one of which was recaptured five months after it was marked at a distance of about 2000 feet from the original site. The other individual was recaptured four times during a six month period in a discrete home range. He was finally recaptured about 1000 feet west of the quadrat nine months after he was marked.

B. *Population Density and Fluctuation*

At the beginning of the study, rice rats were present in rather high numbers. Although both live-trapping and dead-trapping were useful, we soon learned that live-trapping was far more effective for assaying population density. One of the most useful methods for deriving density estimates of mammal populations from live-trap data is the modified Lincoln Index method described by Hayne (1949). This method is based upon several rather standard, although not always valid, assumptions regarding individuals in the population. The method assumes a uniform probability of capture among individuals. Also if the census or retrapping period follows the initial trapping soon afterwards, it assumes no loss in the population due to mortality. It further assumes that no animals have emigrated from the study unit after marking. The Lincoln Index was useful for evaluating several nights' trapping during any one trip. The system was not used over a period of months because it was difficult to meet the mortality assumption on a month to month basis. A somewhat less exacting method than the Lincoln Index was used to evaluate monthly and seasonal changes in population density. The method which we used is based upon trap-night success and per-acre yields from both live- and dead-trapping. One assumption for our method is that the animals may be trapped with equal success throughout the year. For some species in the southern United States, this assumption is not valid (*Sigmodon, Reithrodontomys, Cryptotis*). Our sampling of *Oryzomys* on Breton Island at all seasons suggests strongly that this species is equally susceptible to trapping throughout the year. Ordinarily in the South, as in other areas, it is least easy to trap small mammals in the summer. Providing population densities were high, some of our most successful sampling of rice rats on Breton Island was accomplished during mid-summer and winter. This is probably a reflection of the relatively meager food supply on the island. Conversely, during the summer, we encountered difficulty in obtaining samples of harvest mice, cotton rats, and least shrews from areas on the mainland, even though substantial numbers were present, as trapping success of adults increased in the fall. We have confidence that changes in density of rice rats are well evaluated on the basis of trap-night success and per-acre yield from the live-trapping units.

The summary of trapping results from July 1957 to April 1960, in Table 1 indicates the relative density of rice rats from one month and one season to another. Rice rats were abundant at the start of the field work. The population density remained high late into the winter of 1957-58. A remarkable decline in numbers began in February 1958, and persisted throughout the spring and summer of that year. Recovery began in the fall of 1958, at which time most of the females were pregnant or reproductively active. Thus, the density in the summer of 1958 contrasts sharply with that of 1957. Increase in density continued throughout the winter of 1958-59. This increase was a result of unabated reproduction during the entire winter, in contrast to complete cessation of reproductive activity during the previous winter and spring. The population was again approaching the level of 1957 by spring and summer of 1959. Some idea of the great difference in density that existed

TABLE 1.
*Summary of trapping success*

| Date | Live trap yield | Trap-nights | Trap-night success | Per acre live trap yield | Dead trap yield | Trap-nights | Trap-night success |
|---|---|---|---|---|---|---|---|
| 1957 | | | | | | | |
| July | 10 | 25 | .40 | 4 | 29 | 150 | .19 |
| Aug. | 29 | 160 | .18 | 7.2 | 14 | 100 | .14 |
| Oct. | 17 | 80 | .21 | 6 | 16 | 175 | .09 |
| Nov. | 28 | 160 | .18 | 6.2 | 6 | 90 | .06 |
| Dec. | 43 | 144 | .19 | 6.8 | 19 | 250 | .08 |
| 1958 | | | | | | | |
| Jan.-Feb. | 29 | 336 | .09 | 4.5 | 47 | 488 | .10 |
| Mar. | 6 | 220 | .03 | 0.9 | — | — | — |
| May | 15 | 919 | .02 | 1.1 | — | — | — |
| July | 13 | 2145 | .006 | 0.5 | — | — | — |
| Aug. | 16 | 556 | .03 | 1.1 | — | — | — |
| Oct. | 10 | 567 | .02 | 0.4 | — | — | — |
| Nov. | 3 | 256 | .01 | 0.4 | — | — | — |
| 1959 | | | | | | | |
| Feb. | 55 | 517 | .11 | 2.7 | — | — | — |
| Mar. | 15 | 316 | .05 | 1.9 | — | — | — |
| June | 41 | 554 | .08 | 4.0 | — | — | — |
| Sept. | 9 | 256 | .03 | 1.1 | — | — | — |
| Dec. | 34 | 436 | .08 | 1.5 | — | — | — |
| 1960 | | | | | | | |
| Apr. | 3 | 454 | .007 | 0.2 | — | — | — |
| June | 3 | 504 | .006 | 0.2 | — | — | — |

between the peak and low of the period described is gained by comparing the extremes of trap-success that occurred in July of 1957 and 1958. In July 1957, a total of 175 trap-nights yielded 39 animals, a trap-night success of 0.22. In contrast, a total of 2145 trap-nights in July 1958, yielded only 13 animals, or a trap-night success of 0.01. The incidence of rice rat tracks corroborate the trapping records. From July 1957 to February 1958, tracks were found in abundance, while in the spring and summer of 1958, only one or two tracks were found during any trapping period.

The animals had nearly all died off by late winter and early spring of 1957-58, and not one marked animal was caught in the spring. The only survivors were those born in late autumn and a few during July and August. In a sample of 18 adults taken from March to August 1958, we estimated that 13 of the rats had been born in October or earlier, and 5 in December, on the basis of our known-age growth curves. However, the absence of breeding animals from a large sample taken during December 1957, is good reason for questioning the age determination of the five animals supposedly born within that month. Possibly growth was retarded in young born in late autumn. Barbehenn (1955) suggested a seasonal difference in growth rates of *Microtus pennsylvanicus*. In a habitat comparable to the study areas on South Breton Island, 200 trap-nights yielded no rice rats on North Breton Island in August 1958.

Recovery of the population was underway in the summer and fall of 1958. Breeding continued through the winter and spring of 1958-59. By June 1959, the population was again increasing (0.08 trap success). Reproductive activity declined rapidly during the late summer of 1959, but population density declined slowly until December. The winter of 1959-60 was again unusually severe and long for Louisiana. One cold front after another swept down from the north. Below normal temperatures persisted until the end of April 1960. The population showed much the same trend as that observed in the winter of 1957-58. In contrast to the milder winter of 1958-59, when reproduction continued throughout the year, all reproductive activity ceased from November 1959 on, and there was still no sign of renewed activity by the first week of April 1960. The April sample yielded a trap-night success of 0.007 from 454 trap-nights. Thus, from July 1957 to April 1960, we observed two rather drastic declines in

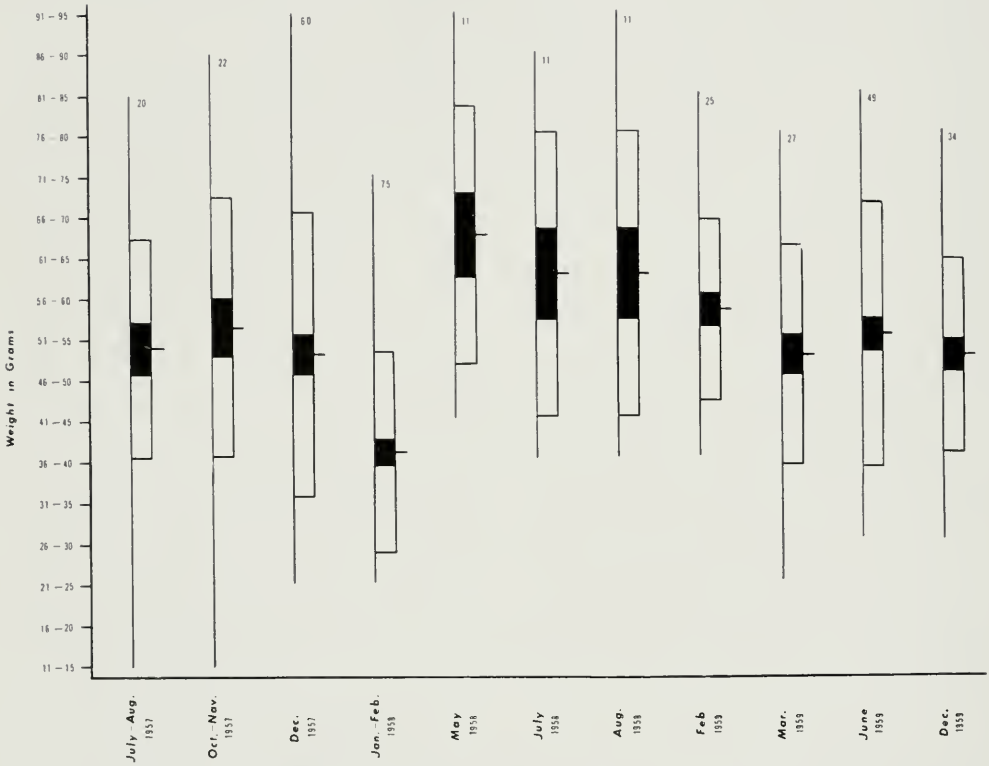


Figure 4. Population weight range of *Oryzomys*. Sample size is indicated at the top of each range. Note abrupt weight loss during the severe winter of 1957-58.

the population, one in the winter of 1957-58, and the second in the winter of 1959-60.

### C. *Population Weight Changes*

During the study every animal was weighed as soon as possible after capture. For each sample of rats, the range, standard deviation, standard error of mean, and mean of the weights was determined (fig. 4). In July-August 1957, the average body weight was 52.8 (± 3.0) grams. The wide range of weights in this sample suggests a considerable range of age in the population. The average weight and range of weights remained almost the same through November 1957. However, in December the average weight was somewhat lower ($x = 51.5$ gms.; $N = 60$) in spite of the fact that the lower weight classes were not represented and the range of high weights was greater than in previous samples.

In the January-February 1958 sample ($N = 75$), the average body weight was 40.9 (± 1.4) grams. The average body weight per rat in this sample was 10.6 grams lower than in the December 1957 sample. We feel that this difference in average weight was largely a result of individual weight loss during the winter. This conclusion is supported by a small sample of rats from one of the live quadrats that were recaptured and weighed during both sampling periods:

| Animal No. | Sex | Dec. Body Wt., gms. | Jan.-Feb. Body Wt., gms. | Diff. |
|---|---|---|---|---|
| F1E7 | ♂ | 56 | 48.7 | —7.3 |
| F3E7 | ♀ | 41 | 35.6 | —5.4 |
| F4E2 | ♂ | 36 | 27.8 | —8.2 |
| F2E1 | ♀ | 35 | 39 | +4.0 |
| F2E4 | ♀ | 46 | 43 | —3.0 |

This is in contrast to our data from other seasons in which recaptured individuals generally show weight gains from one sampling period to the next.

The low average weight in January-February coincided with a rapid decline in numbers of *Oryzomys* on the island. By May 1958, the average weight had risen to 64.8 (± 5.0) grams. A similar but less drastic decrease in average weight occurred in samples taken during the less severe winter of 1958-59.

### D. *Breeding Season*

One of the most variable aspects of the reproductive phenomena was the extent of the breeding season. In 1957, rice rats were breeding when we began work in July, but had ceased by the end of October. No further reproductive activity was recorded until May 1958, and from this time animals were breeding throughout the summer, fall, and winter of 1958, and into the spring and summer of 1959. A surge of reproductive activity was noted in the early months of 1959. During the first three months of this year, all of the females that had attained at least subadult status were either pregnant or lactating or both. Population density increased during this period, but tended to slow down in the summer months, possibly due to a depressing effect of high temperatures on reproductive activity. Odum (1955) suggested that high summer temperatures in Georgia were responsible for depression of reproductive activity in *Sigmodon*. The incidence of estrous, pregnancy, and lactation in adult and subadult females gives some indication of the ebb and flow of reproduction throughout the seasons and years of the study (fig. 5).

### E. *Litters Per Year*

According to Svihla (1931), a female *Oryzomys* in Louisiana might bear as many as nine litters per year. This may be theoretically possible on the basis of the gestation period, 12-month breeding season, and average longevity of more than one year. However, our data show that this is an unrealistic figure. Recapture data from live-trapping quadrats suggest that the average longevity is probably about seven months. There may be a nonbreeding period extending for six months as was the case during the winter of 1957-58 and 1959-60. Our data on known-age rice rats in the laboratory indicate that the vaginas of young females open at an age of 40-45 days coincident with the acquisition of subadult pelage. Males mature sexually at about the same age, on the basis of size and scrotal position of the testes. This is somewhat younger than the age (57 days) of sexual maturity quoted by Conaway (1954) for female *Oryzomys* from Tennessee. If we assume that the average female has at most six months of reproductive activity during her life span, the

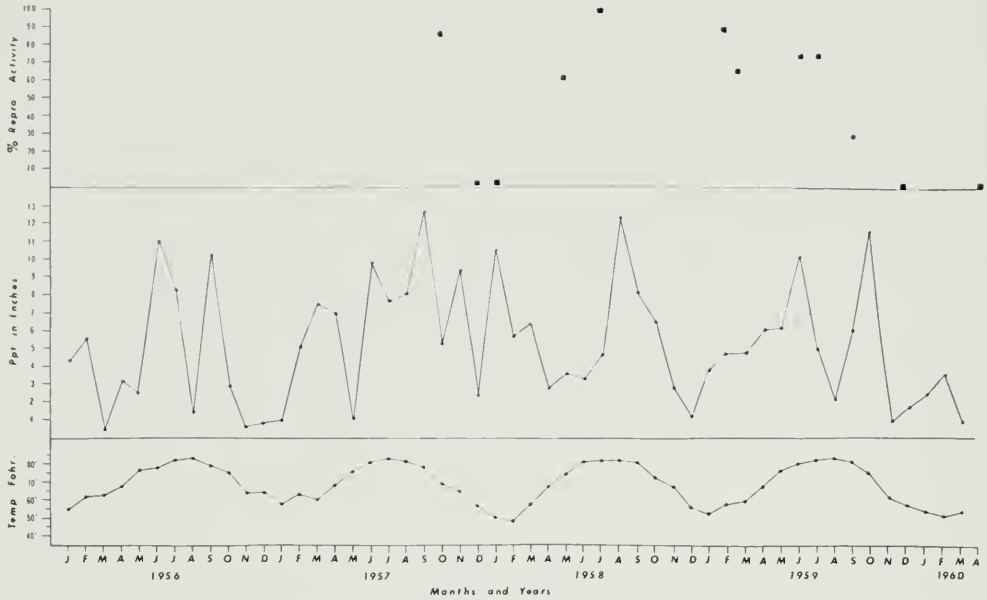


Figure 5. Climatic data in relation to reproductive activity in female cotton rats. Data on average monthly temperature and total monthly precipitation are taken from the U. S. Weather Bureau records from Burrwood, La. Reproductive activity in females is based on live and dead samples combined.

maximum number of litters produced by the average female is five or six. A female may produce far less than the maximum number of litters when subjected to inclement weather or food shortage as, for example, the six-month non-breeding period during the winter of 1957-58.

### F. *Litter Size*

Most of the data on litter size have been obtained by counting embryos of pregnant females in dead samples. Additional records were obtained from pregnant animals captured alive and brought to the laboratory where they gave birth.

The mean number of embryos of 20 adult females collected from 1957 to 1959 is 4.8. Ten of these counts were recorded from July to November 1957. The mean for this group is 3.7, with a range from 2 to 5. The remaining ten embryo counts were recorded during the period May 1958 to June 1959. The mean for this sample is 6.0, with a range of 4 to 7. This difference in average litter size occurred during contrasting phases of population growth. The low litter size data from 1957 were obtained during a period of high density. The other sample, however, was collected after the population had declined and had begun to increase from a very low density. The difference in the means of these two samples is highly significant at the 0.01 level (Table 2).

### G. *Ovarian Activity*

In eleven pairs of ovaries from reproductively active adults taken in 1957, the mean number of corpora lutea per pair was 4.5 (range 3-8). Nine pairs of ovaries from adults taken in 1958-59 had a mean corpora

TABLE 2.
*Comparison of embryo counts in adult Oryzomys 1957-1959*

| Sample | N | d.f. | Mean Value | Sums of Squares | |
|---|---|---|---|---|---|
| 1957 | 10 | 9 | 3.7 | 145 | $t = 3.776$ |
| 1958-59 | 10 | 9 | 6.0 | 370 | $t$ .01, 18 d.f. $= 2.552$ |

TABLE 3.
*Comparison of ovarian activity in adult Oryzomys 1957-1959*

| Sample | N | d.f. | Mean Value | Sums of Squares | |
|---|---|---|---|---|---|
| 1957 | 11 | 10 | 4.5 | 245 | t = 2.22 |
| 1958-59 | 9 | 8 | 7.6 | 576 | t .05, 18 d.f. = 1.734 |

lutea count of 7.6 (range 4-12) per pair. The difference was significant at the .05 level (Table 3). This trend coincides with similar differences in embryo counts from the two periods. Apparently rice rat litter sizes are directly related to the number of ova released. Litter size in the rice rat may be controlled largely by the activity of the ovaries rather than by resorption rates, implantation failure, etc. Estrogen secretion and the associated gonadotrophins of the anterior pituitary (FSH and LH) probably control the number of ova released and thus the litter size.

Ovaries examined during nonbreeding periods were considerably reduced in size and lacked maturing follicles. In some females that were reproductively active only one ovary, usually the right, was functional, the other being greatly reduced in size with no follicular development (figs. 6, 7). Even when both ovaries were functional, the right often showed greater activity on the basis of corpora lutea and albicantia counts. Fifty-six percent of the corpora were found in the right ovary in contrast to forty-four percent in the left.

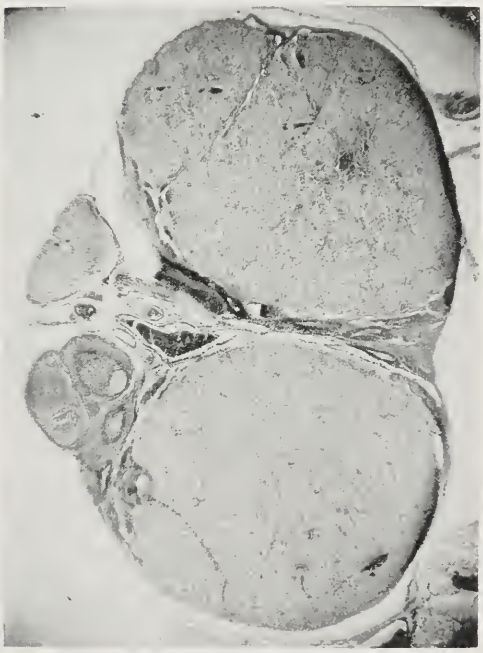

Figure 6. Photomicrograph showing the corpora lutea of the active right ovary of an adult pregnant *Oryzomys*.

Figure 7. Photomicrograph showing the relatively inactive left ovary of an adult pregnant *Oryzomys*.

Corpora lutea of pregnancy averaged 1.1 mm in diameter while corpora albicantia averaged 0.5 mm. Atretic follicles were commonly observed in specimens taken in fall and winter.

### H. *Growth Rates*

Nearly always the age of a mammal is difficult to determine. More information on the close relationship of age with physiological processes and behavior may lend greater insight into the problems of population ecology.

Growth rate data have been recorded from a total of 49 known-age rice rats in the laboratory. Animals were examined at weekly and bi-weekly intervals. At each examination, the following data were collected: weight, total length, tail length, hind foot length, ear length, pelage stage, and reproductive data. Developmental changes in behavior were also observed. The growth rate curves in weight and in total length (fig. 8) are constructed on the basis of several hundred observations of a large sample of animals. An enlightening aspect of these data is that rice rats continue to grow substantially for a considerable period of time, perhaps throughout the average lifetime of an individual. Our known-age data do not extend beyond 270 days of age. However, the measurements of several individuals recaptured in the field that were at least a year old, were considerably larger than our oldest laboratory animals. For example, a subadult male originally captured in October 1957, was recaptured for the last time 20 months later in June 1959. At final capture the animal measured 262 mm in total length, which is considerably larger than the size attained at one year (fig. 8). This extended growth period may well account for the variation in size noted in taxonomic series by some workers (Goldman, 1918; Paradiso, 1960).

We were anxious to compare the growth rates in the field with those of laboratory-reared rats. Accordingly, eighteen young rice rats born of Breton Island females, were toe-clipped and released on the island in June 1959. Only one of these individuals was subsequently recaptured. We have recently gained further information on field growth rates from animals marked as juveniles and subsequently recaptured. One such animal was marked and recaptured on the same dates that a known-age animal was released and recaptured respectively. These data agree well with our laboratory growth rates (fig. 8).

Once adult status has been attained, body weight *per se* is not an adequate criterion for age. The variation in weight of those animals 150 days of age and older may be attributed to fat accumulation, reproductive activity, and other factors. Increases in total length, however, seem to show less variation, even at older ages. If age increments of one or two months are assigned, the reliability of aging from growth curves seems to be high.

### I. *Age Composition*

Evaluation of age composition of live and dead samples was based on the following criteria: weights, total length, reproductive condition, and pelage stages. Comparisons were also made with data collected from known-age animals in the laboratory. None of these criteria was used exclusively or absolutely, but was evaluated along with other characteristics. Total length was, by far, the best criterion for age determination. Pelage condition and degree of development of reproductive organs facilitated age determination of juvenile and subadult groups.

A sharp division between subadult and adult groups was difficult to define. An intermediate group, (subadult-adult) was thus established. Approximate measurement criteria for separating age groups were as follows:

Juvenile — TL up to 210 mm, wt. up to 32 gms.

Subadult — TL 205-220 mm, wt. 30-50 gms.

Subadult-adult — TL 220-230 mm, wt. 50-55 gms.

Adult — TL 230+ mm, wt. 55 gms and over.

The age composition of rice rats at various periods from 1957-1959 are indicated in figure 9. The trends in composition reflect closely the changes observed in reproductive activity and density.

### J. *Behavior*

Our trapping procedure revealed that rice rats are active only at night. We have observed neither activity nor trapped rats during daylight hours even though traps were left set throughout each 24-hour period. Greater activity on cloudy and rainy nights was indicated by higher trap success. Blair (1951) noted that *Peromyscus polionotus*

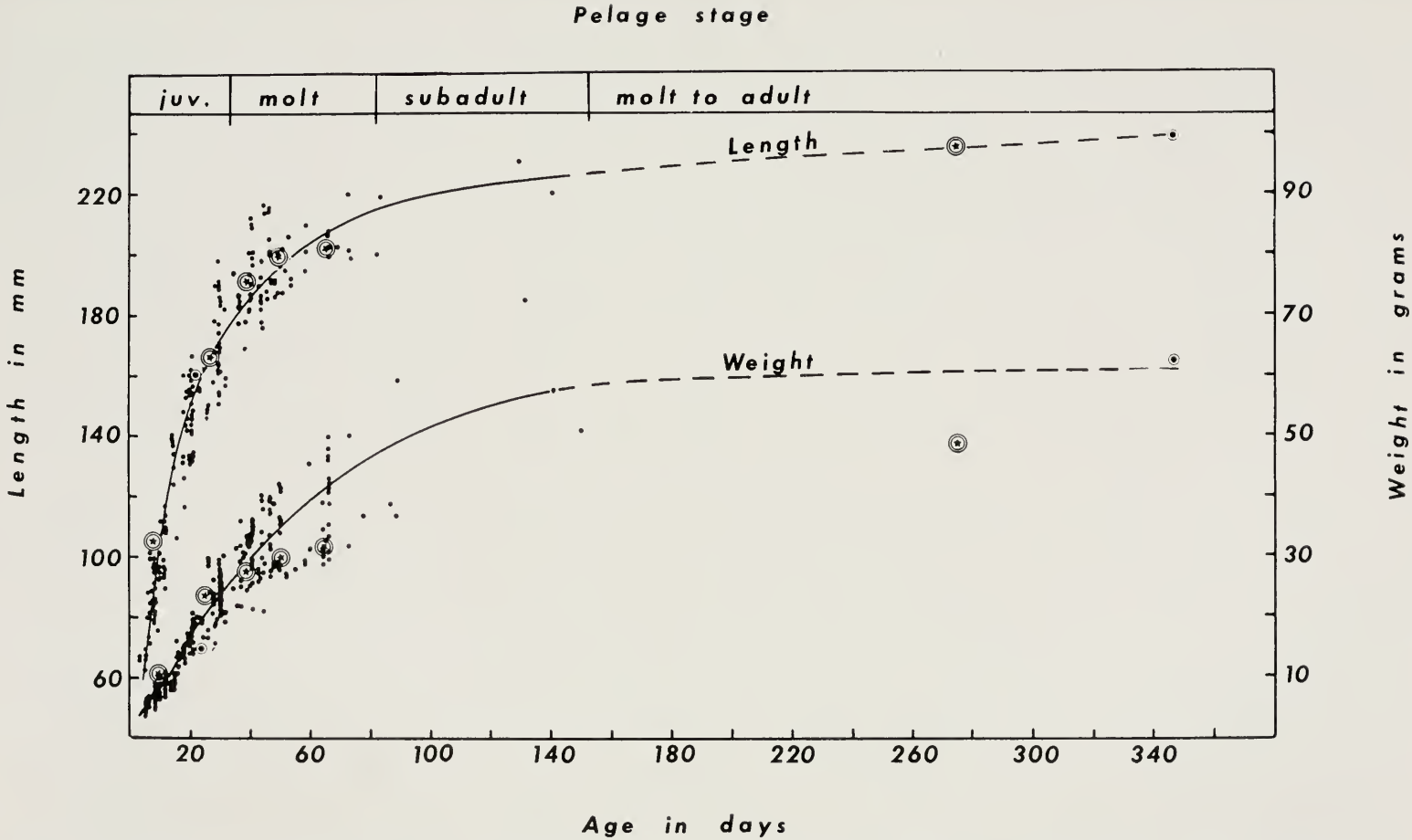


Figure 8. Growth curves in total length and body weight derived from animals in the laboratory. Age ranges for pelage stages are indicated at the top of the figure The starred circles represent one of the animals (A) reared in the laboratory, released on the island at 65 days of age, and recaptured six months later. The large solid center circles represent a male that was initially captured on the island at the time the above rat (A) was released and judged to be 8 weeks old on the basis of measurements and pelage criteria. He was subsequently recaptured at an estimated age of 340 days.

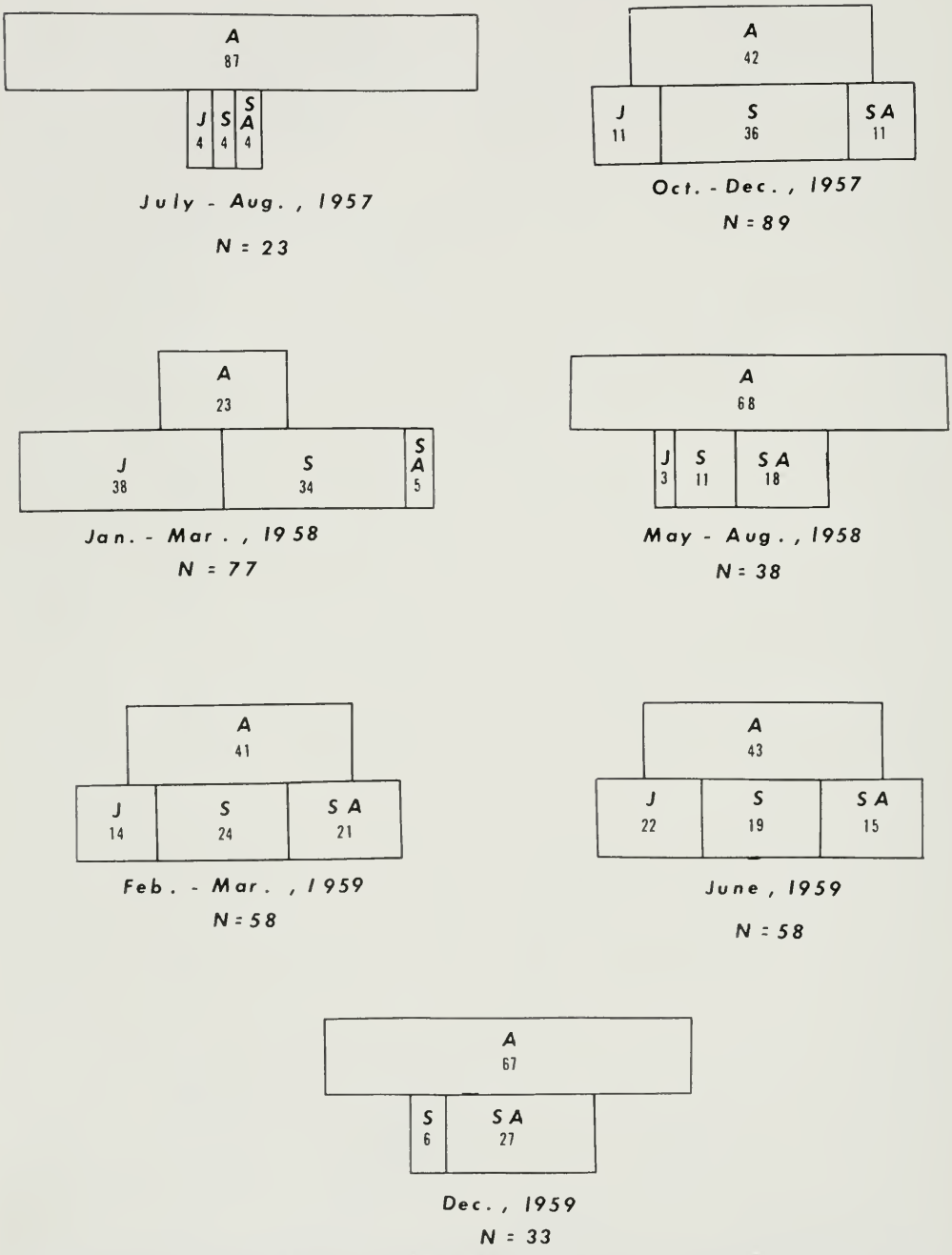


Figure 9. Age composition of some *Oryzomys* samples from Breton Island. The letters in blocks represent age classes, juveniles: J; subadults: S; subadult-adults: SA; adults: A. Numbers in block represent percentage of respective age categories in each sample. The abundance of young animals in the Jan.-Mar. 1958, sample may be a reflection of stunted growth as a consequence of the severe winter.

on Santa Rosa Island, Florida were much more active on cloudy nights than on moonlit nights.

We conducted systematic searches for nest sites in the sedge community. A number of nests were found, usually located on high ground either in a hollow log or under pieces of driftwood. Nests that housed a single rat were rather elongate structures, about 2-3 inches wide and 5-6 inches long, of loosely interwoven grass. One nest was located at the base of a thick clump of sedges. During winter several large oval nests about 6 inches in diameter were found under boards. One of these contained five large rice rats; two other nests contained four and three individuals. Such communal nests were observed only during winter.

One instance of homing was recorded. Eight animals were released 250 feet east and west of the trapsite in November 1957. One juvenile male returned from the west. He was then released 250 feet east of home and returned the following night. On the third night, he was released 250 feet north of home, and failed to return.

Although we did not see evidence around nest sites of food caching, a considerable quantity and variety of seeds was found under one of the bunks when rice rats invaded the cabin in the winter of 1959-60. This was the only time that the cabin was invaded and was coincident with high populations. During the same period oil company employees on North Breton reported an abundance of rice rats around their garbage area.

By following tracks of *Oryzomys* in the sand in winter, we observed considerable digging around the bases of grass and sedge clumps, presumably in search of food.

### K. *Food Habits*

Sixty-one stomach contents were examined from various seasons to determine food habits (fig. 10). The food eaten throughout the year implies an extremely varied diet, thus the difficulty of generalizing about any one period of sampling. We were surprised to find the mycelial threads and spores of the fungus *Endogone* in the stomachs of November, February, and May samples. Hamilton (1941) mentioned the presence of this fungus in several mammals, *Synaptomys cooperi, Sorex fumeus, Sorex cinereus, Blarina brevicauda. Peromyscus leucopus* and *maniculatus* and *Clethrionomys gapperi.* He further commented: "All of these species occupy, at the same time, the stratum where this fungus grows, and it appears to be a food of more than passing importance to the several species." At least two different types of fungi from the family *Endogonaceae* were recognized, *Endogone* and an unidentified genus. The occurrence of sand with this fungus in the stomachs is probably a result of *Endogone's* subterranean habit. Plant parts too well chewed to permit identification made up a large portion of the contents. Stem and leaf parts and unidentified seeds of numerous plant species were abundant. Flower parts occurred in eight different samples. Insects of various types were frequently encountered. The stomach of one rat collected in December had eleven larvae. Two moths, a butterfly, some lepidopteran scales, spiders and aquatic insects, a centipede and the chitinous parts of many unrecognized insects were found among the arthropod portions of the contents. Six rice rat stomachs contained seven insect wings, although larvae constituted the greatest bulk of the insect remains. The size of two snail radulae taken from a specimen collected in February suggests that the shell size was certainly over five inches, indicating that rice rats sometimes forage along the beach. Another stomach of a specimen collected in the same month contained flesh and scales of a small fish. A gill-like structure, probably from a mollusk, was found in a July sample.

### L. *Adrenal Gland Weights*

Adrenal glands were removed and weighed from all animals collected for dead samples. To compare adrenal weights from rats of varying sizes, we converted each pair to milligrams of adrenal weight per gram of body weight. A summary of the adrenal weight data is presented in Table 4. A considerable increase in adrenal weight occurred from December 1957 to February 1958, particularly when compared to adrenal weight of August 1957. The increase of adrenal weight from December to February is greater when expressed as milligrams per gram of body weight than when expressed as gross adrenal weights (Table 4). General body weight loss throughout the popu-

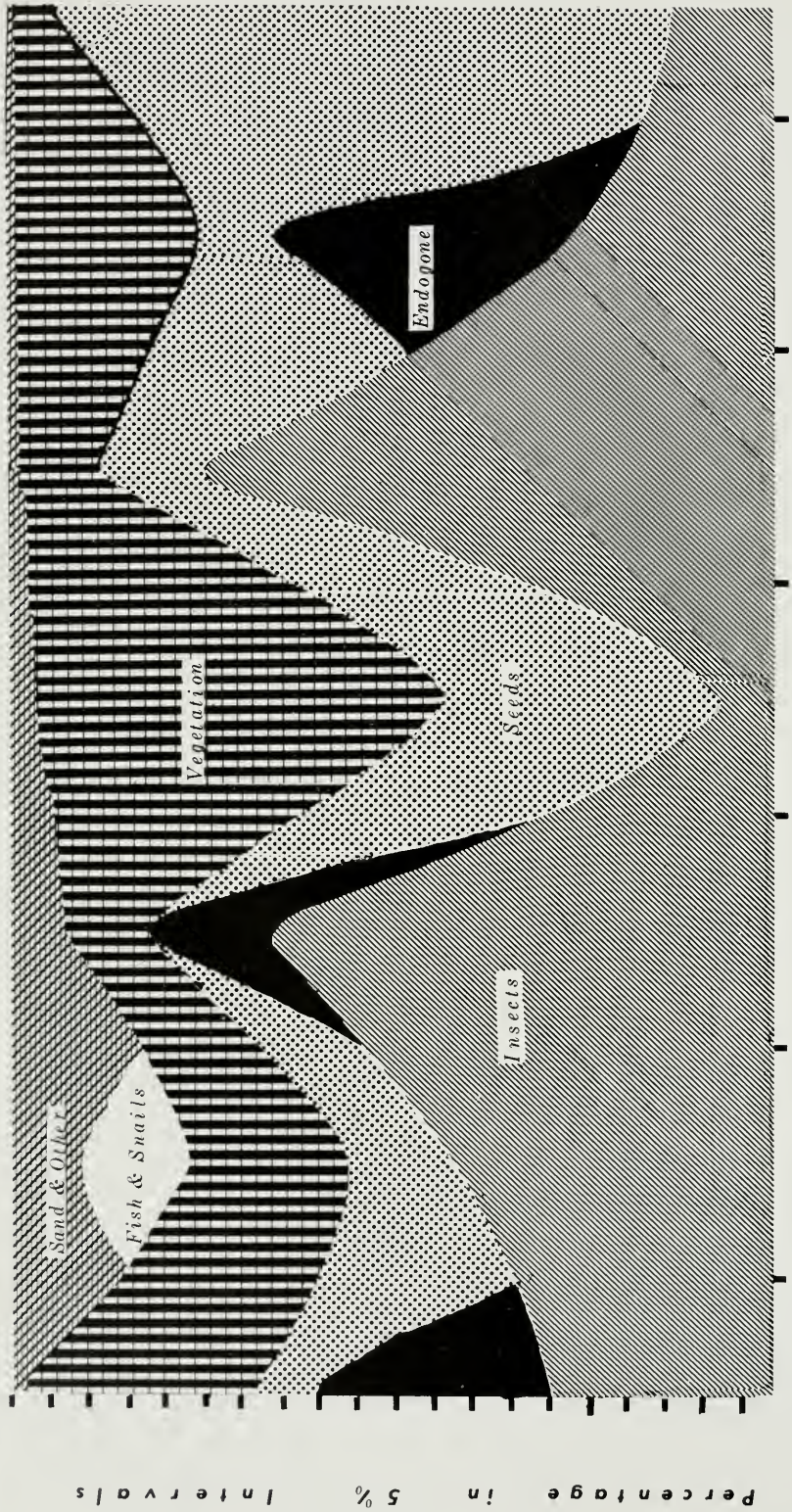


Figure 10. Food habits of *Oryzomys* on Breton Island as determined by stomach analyses of 61 animals from various seasons, 1957-1959. An analysis of year to year food habits is in progress.

TABLE 4.
*Adrenal weights from samples of Oryzomys on Breton Island*

| Date | Mean adrenal wts., mgm | Range | Mean body wts. gms | Mean adrenal wt./gm body wt. ♀ | ♂ | Mean adrenal wts. mgm/gm ♀ and ♂ | N |
|---|---|---|---|---|---|---|---|
| Aug. 1957 | 6.0 | 3.8- 8.0 | 59.2 | — | .1114 | .1114 | 8 |
| Dec. 1957 | 8.5 | 3.9-18.3 | 39.8 | .208 | .212 | .2047 | 14 |
| Feb. 1958 | 14.4 | 6.4-28.0 | 43.9 | .322 | .320 | .3208 | 31 |
| May 1958 | 15.4 | 11.5-19.8 | 60.8 | .331 | .190 | .2905 | 5 |
| Jul.-Aug. 1958 | 7.3 | 3.5-10.8 | 49.3 | .220 | .167 | .1720 | 15 |
| Dec. 1959 | 19.4 | 11.2-36.0 | 48.9 | .396 | .379 | .3957 | 25 |

lation during the winter accounts for this.

There was general decline of adrenal weight in 1958. At this time populations were recovering from very low density. We do not have adrenal data for the winter of 1958. However, a sample of 25 pairs of adrenals from December 1959, indicates that weights had again increased substantially (fig. 11). These high weights, as in 1957-58, accompanied fairly high densities as well as bad weather conditions.

## V. DISCUSSION

The causes of population fluctuations have been variously attributed to a number of environmental phenomena. Climatic changes, inter- and intra-specific competition, disease, the availability and nutritive value of food are but a few. Pitelka (1958) divided theories of population cycles into two schools of thought: (1) those which contend a close relationship between population changes and extrinsic variables, and (2) those

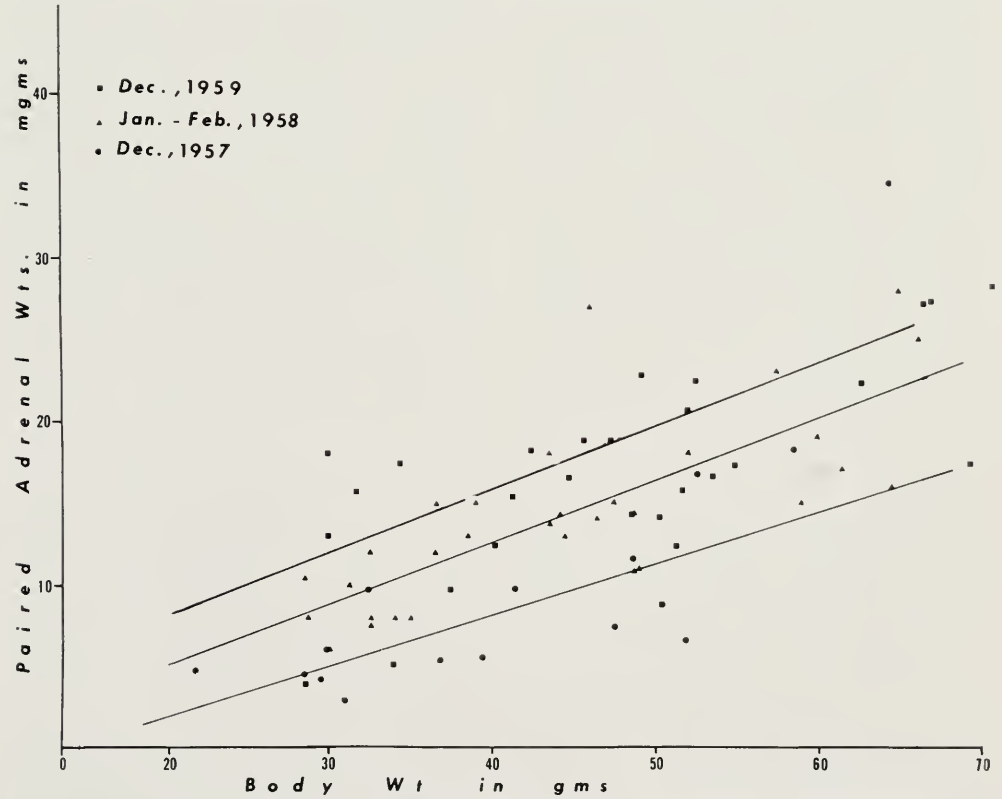


Figure 11. Distribution and regression lines of rice rat adrenal weights from three samples, showing relationship of adrenal weights to body weights in animals of various sizes and ages.

which emphasize an intrinsic mechanism.

In one of the early studies of population cycles, Hamilton (1937) suspected murine epizootics as a primary causative agent in reducing mouse populations.

Lemmings on the arctic tundra have been studied by Pitelka (1957), who pictured an inseparable trio of biotic interaction: lemmings, soil, and vegetation, "Winter cuttings of vegetation and the resulting removal of food and cover expose peak densities of lemmings to predation, which is the usual agent figuring in the inevitable decline of the population." Frank (1957) agreed with Christian's (1950) earliest hypothesis though differed on one essential point. Frank attributed the intrusion of harsh frost periods accounting for the abruptness of the decline as the ultimate trigger eliciting the crash of vole populations. Such climatic importance is closely allied to our concept of rice rat population fluctuations.

Chitty (1960) suggested another theory. He believed that some self-regulating mechanism has evolved in voles. Under special circumstances this mechanism makes them more susceptible to mortality factors by a deterioration in the quality of the population.

Five instances of high populations coincident with the flowering of bamboo in South America and Malagasy Republic (Madagascar) are discussed by Grassé (1955). Tanaka (1956, 1957) reported that bamboo flowering does not always coincide with vole peaks in Japan.

If we are to properly evaluate the proposed intrinsic mechanisms influencing populations, we must first be fully cognizant of the assumptions and experimental data that have formed the basis for such theories. The adreno-pituitary exhaustion theory proposed by Christian (1950, 1956a, 1956b, 1959a, 1959b) has gained greater acceptance and popularity than any other recent work on intrinsic factors.

Christian's theory is based in part upon the premise that he effectively isolated density as the single variable responsible for changes in adrenal cortical activity, reproduction, and other physiological processes in caged populations. In house mouse populations varying in density from one to 16 mice per square foot, he found a progressive increase in adrenal size. He attributed this increase and the attendant changes in reproductive activity to socio-psychological stress induced by high density. First, we must consider the magnitudes of densities actually involved in the experiments. Sixteen mice per square foot area approximates 697,000 mice per acre by extrapolating the upper limit of density at which increased adrenal weights were still manifest. Densities of 32 mice per cage are equivalent to 1,394,000 mice per acre. Caged densities at which adrenal hypertrophy occurred, in apparent direct response to density, were obviously many times the maximum densities encountered even in natural plague populations. One of the densest populations on record is described by Hall (1927) who estimated 82,280 animals per acre in a California plague of house mice and voles. Densities of Christian's 42 square foot cage (17,000 per acre) are far above the usual peak numbers encountered in rodent populations.

Bodenheimer (1957) studied *Microtus guentheri* for five years and found, contrary to other caged studies, that in a series of ten, two square meter cages these mice "took to each other very well." "In the few cages where fighting led to a few killings, its occurrence was independent to the intial vole number." He concluded that the intensity of fighting is as much dependent upon individual sociability as upon environmental factors. "Periods of heavy killing were not preceded by periods of unrest in the cages." Three to six months often separated periods of fighting.

Chitty (1960) remarked, "contrary, therefore, to what some authors appear to believe, useful results will not necessarily follow from keeping animals at a density several hundred times that occurring in nature, and at the same time failing to provide a substitute for their runways and cover." Another factor that defies evaluation and yet must certainly exert its effect upon caged mice is the confinement of the cage itself which forces contact among the occupants; a condition that is certainly never approached in the field.

Under such high density and confinement, if social stress is an important mechanism in population dynamics, one would expect the most drastic responses to manifest themselves by changes in reproduction, mortality,

and health via the adreno-pituitary system. How does the magnitude of response in the laboratory compare with that of the field? In natural populations, confinement is lacking, densities are lower, and there is less assurance of contact. Thus the adrenal response to social stress in Christian's caged populations should be greatly magnified. Such, however, is not the case. The maximum amount of increase in adrenal weights in Christian's mice with increasing density is actually small (25%), particularly when compared with the magnitude of adrenal weight increase (95%) that accompanies merely the onset of reproductive activity in female cotton rats (Table 6).

Christian supported his theory through the interpretation of his caged animal data on *Mus* (1955, 1956a), wild Baltimore *Rattus* (Christian and Davis, 1955, 1956), natural populations of *Microtus* (Adams, Bell and Moore, unpublished, Christian, 1959b), and evidence from Louch (1956, 1958) and Green, et al (1938, 1939). Green's work was recently found deficient in its support of the adreno-pituitary hypothesis (Chitty, 1959).

Louch (1958) studied two populations, one at Mudd Lake and another at Hammersley Marsh. He stated that two factors brought about the greater adreno-cortical activity observed in the fall of 1952 in both areas. One of these, the drought conditions of that fall, appeared to act in both areas to bring about increased adreno-cortical activity. The other factor, high population density, was present only in the Mudd Lake area and appeared to increase the adreno-cortical activity of the mice to significantly higher levels than at Hammersley Marsh. Louch suggested that the drought conditions and the high population density present in the Mudd Lake area may have had an accumulative effect resulting in significantly higher adrenal weights and lower eosinophil counts than in the area where drought alone was a factor. Thus Louch presented data in which density may be isolated, in terms of adrenal weight, from climatic impact, under natural conditions.

We shall therefore compare Louch's confined population with his two wild populations and use the adrenal weights under confined conditions as a yardstick for social pressure due to density. Louch offered the following information on adrenal weights in cages (6′ x 25′) and in the wild populations (Table 5).

Let us assume that 0.149 mg/gm of body weight (the mean adrenal weight of Hammersley and Mudd Lake populations at low density) represents a basic unstressed adrenal weight for *Microtus*. The mean difference between the basic adrenal weight (0.149) and the mean Hammersley adrenal weight under drought conditions (0.194) is 0.045. This value (0.045) thus represents the increased weight of the adrenals due to drought. In the same way 0.081 represents the mean adrenal weight increase due to drought and density at Mudd Lake (0.230 — 0.149 = 0.081). We arrive at the density value of 0.036 (0.081 — 0.045 = 0.036) if Louch's interpretation of the data is accepted, *i.e.*, that the Hammersley population was varied by drought only (since

TABLE 5.
*Adrenal weight data from caged and natural populations of Microtus pennsylvanicus (Louch, 1956, 1958)*

| Pen | Pop. end point All animals killed | Approx. high population | Mean adrenal wt. ♂ (mgm/gm body wt.) | Diff. of mean adrenal wts. among cages (mgm/gm body wt.) |
|---|---|---|---|---|
| A | 15 | 28 | .104 | .04 (B) |
| B | 42 | 53 | .144 | .06 (C) |
| C | 20 | 67 | .086 | –.02 (A) |

| Period | Mean ad. wts. Hammersley (drought only) (mgm/gm body wt.) | Mean ad. wts. Mudd Lake (drought & density) (mgm/gm body wt.) |
|---|---|---|
| Nov.-Dec. 1952 | 0.194 | 0.230 |
| Feb.-Nov. 1953 | 0.152 | 0.145 |

density was low) and that the Mudd Lake population was affected by drought and density.

The value (0.045) which we have attributed to drought is thus equal to the adrenal weight difference (0.04) between the highest density (Pen B) and the lowest (Pen A) (Table 5). These data raise the question: why attribute the causes of adrenal enlargement to social stress when climate alone seems to play so great a role?

Still another comparison may be made. The mean adrenal weight (0.145) of the Mudd Lake population at low density, in the absence of drought, is equal to the mean adrenal weight (0.144) of the highest cage densities( Pen B). Thus where density is non-contributing, the high adrenal weight under natural conditions is presumably a response to the environment.

Christian (1959b) stated: "There must be a maximum amount of space that would still permit the mice to interact. . . ." One might logically conclude that space may be sufficiently unlimited to render social interaction ineffective in natural populations.

Christian (1959a) recognized the import of environmental vicissitudes by establishing his "unit of social pressure". He considered it to be a variable unit from one population to the next, depending upon the existing enviromental conditions as well as the density. The unit of social pressure is thus defined as the net effect of favorable or unfavorable extrinsic factors mediated through the common pathway of social stress among the individuals. Thus, the "unit" is placed upon a sliding scale dependent not upon density *per se,* but upon environmental conditions.

Environmental factors are admittedly of great importance. Is Christian justified, however, in mediating all such factors through the common pathway of social stress? Christian himself (1959a) recognized the significance of work by Srebnik, Nelson, and Simpson (1958) regarding the direct effect of protein deficiency on the reduction of circulating gonadotrophins. Dale (1955) presented evidence that calcium intake may have a direct effect upon ovulatory rates and viability of eggs in pheasants. Bodenheimer (1949) did a series of experiments with *Microtus.* He used a variety of grain and mixed feeds, and concluded that differences in nutrition find their expression in differences in fertility. These data preclude the necessity of postulating an indirect relationship between the environment and the animal.

Christian (1959a) defended his hypothesis on the basis of a commonly held assumption that some single factor common to all populations underlies the causes of fluctuations. He clearly stated a common pathway which he has chosen on the basis of his field and laboratory data: "socio-psychological factors are the principal stimuli for the adrenal and reproductive responses as these are factors common to all populations." Is socio-psychological stress the only factor common to all populations?

Both nutritional and climatic factors are equally common to all animal populations. Wild populations are constantly responding to environmental vicissitudes. Logically we assume that the more significant stresses upon the population will be generated directly from the environment with social contacts and relative density at low levels as compared with caged conditions.

The limited distribution and abundance of food plants on Breton Island, the unsheltered nature of the sedge community, and the severe wind and wave action, coupled with a water table just beneath the surface of the sand, all contribute to the sub-optimal nature of the habitat. Despite the highly omnivorous food habits of *Oryzomys,* plant food when abundant becomes predominant in the diet. Conversely, during the winter, stomachs contained largely insects and fungi (Endogonaceae) and few vegetative parts.

As the numbers of rice rats rise in response to favorable climate and abundance of food, competition for nest sites becomes progressively acute. Suitable sites on the island are limited largely to logs and debris located on high ground and to clumps of vegetation beyond the reach of high water. The impact of marginal environment combined with the hazards of winter may impose considerable stress on the population. Falling temperatures lead to greater nutritive needs in the face of depleted food reserves. The population is likely to suffer heavy losses with the onset of a severe winter, the attendant food shortages and delay of spring growth.

In December 1957, impending disaster

to the population was manifested by the low average weight in a sample of 62 animals. The emaciated condition of 75 rats was visibly evident in January - February 1958. Most of the animals examined during this sampling period are described in the field notes as being thin and "bony" and pelage in poor condition. The mean weight loss for the entire sample compared to the December 1957 collection was 10.6 grams (fig. 4). Poor physical condition thus prevailed throughout the population just prior to the sharp decline in early 1958.

The magnitude of adrenal weight increase in our *Oryzomys* population (based on milligrams per gram of body weight) is of the order of 200 per cent from low to even moderate densities (7-10 per acre). One is tempted to conclude that the effect of social interaction on adrenal weight changes are overshadowed by other environmental effects in the light of subtle adrenal weight changes (25%) observed in extreme cage densities as compared with those of much lower densities found in nature. At what point then, does high adreno-cortical activity precipitate a measurable response in the population? The concept that adrenal weight serves as a yardstick for the causes of population fluctuation has received great emphasis. However, in our review of the literature we have been impressed by the inconsistencies of the data. For example, Mullen (1960) in a presentation of aberrant adrenal weight data from a natural population questions the reliability of adrenal enlargement as a criterion of population density "stress".

The rise and fall of the *Oryzomys* population on Breton Island and the coincident change in adrenal weights can clearly be interpreted in the light of Christian's theory of socio-psychological stress. But is there not an equally valid hypothesis on the basis of our data? We can just as well explain the increase in adrenal size and complete cessation of reproduction, as well as weight loss in the population, on the basis of climate and food. The winter of 1957-58 was one of great severity and duration in Louisiana. The highest adrenal weights occurred in late winter and early spring. Depleted food supplies coupled with low temperatures imposed an unusually severe stress upon the population. One has only to postulate that the late initiation of vegetative growth in the spring, coupled with prolonged inclement weather, presented a condition of poor nutrition and low temperature. These conditions directly affected the reproductive physiology and health of the population. Our interpretations of the interrelationships between environmental factors and population density is presented in figure 12.

Our forementioned conclusion is further substantiated by data collected at the same time for *Sigmodon* populations on the mainland of Louisiana and Texas. During the period 1957-58, populations of *Sigmodon* in southern Louisiana study plots of 5 acres each were at low to moderate densities (3-6 / acre) in oldfield habitats. In this form as well as other small mammal species of the mainland, all reproduction ceased for an extended period from November 1957 to May 1958, the identical period of non-reproductive activity expressed by our island population of *Oryzomys*.

A sample of 20 adrenal pairs from a cotton rat population at low density in Louisiana during July-August 1958, had a mean weight of 18.7 mgms (Table 6). On the other hand, a sample of 32 adrenal pairs from a plague population (several hundred per acre, Davis, 1958) of cotton rats in Texas during January 1959, had a mean weight of 12.6 mgms. This same population was sampled in March 1959. At this time 51 pairs of adrenals had a mean weight of 18.1 mgms. Reproductive activity in this population began in late April 1959, and a sample taken in May yielded 100 per cent pregnant females. Thirteen pairs of adrenals from this same sample had a mean weight of 27.5 mgms. However, the weights of female adrenals in this sample were much higher ($\bar{x} = 39.8$ mgms) than those of males ($\bar{x} = 16.9$ mgms).

The foregoing data imply that density and contact are not necessarily important factors influencing adrenal weight changes in natural populations. It is difficult to imagine greater stress due to density and contact in a natural population than that which was present at peak densities in the Texas plague. At night in a short walk through the plague infested area, one could witness hundreds of cotton rats scurrying about. Often three or four animals were seen huddled together in the mouth of a burrow,

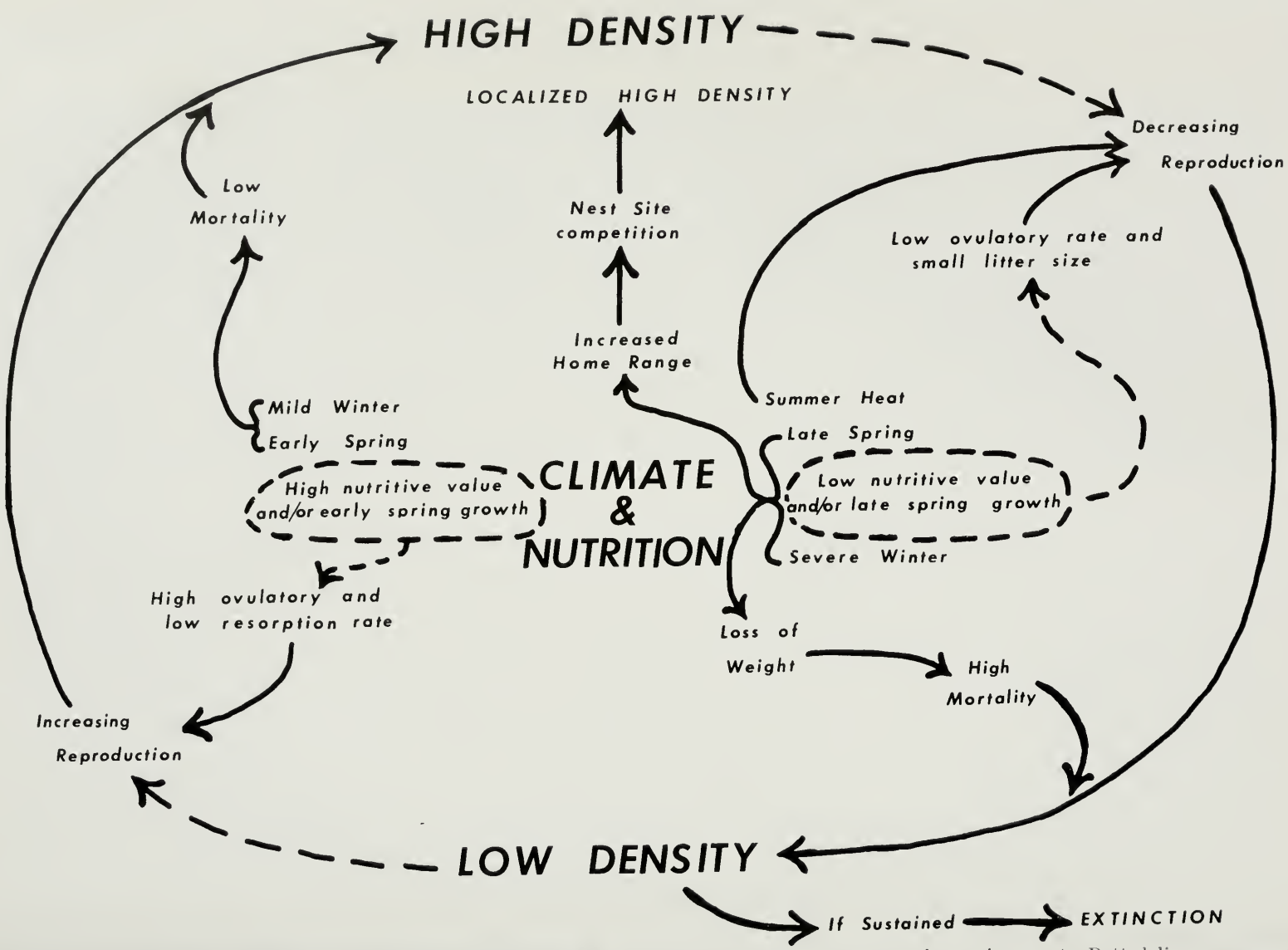


Figure 12. Schematic diagram of the Breton Island *Oryzomys* population and its response to the environment. Dotted lines represent hypothetical aspects of the scheme.

TABLE 6.
*Adrenal weights of Sigmodon hispidus*

| | Texas, Jan. 1959 (high density) | Texas, March 1959 (high density) | Texas, May 1959 (low density) | Louisiana, June-July 1958 (low density) |
|---|---|---|---|---|
| | N = 32 | N = 51 | N = 13 | N = 20 |
| Mean combined adrenal weights (mgms) | 12.5<br>♀ = 12.4<br>♂ = 12.6 | 18.1<br>♀ = 20.25<br>♂ = 16.03 | 27.47<br>♀ = 39.8<br>♂ = 16.9 | 18.7<br>♀ = 22.1<br>♂ = 15.4 |
| Mean mgms adrenal wt/ gm body weight | 0.136<br>♀ = 0.156<br>♂ = 0.123 | 0.224<br>♀ = 0.236<br>♂ = 0.193 | 0.213<br>♀ = 0.320<br>♂ = 0.121 | 0.234<br>♀ = 0.311<br>♂ = 0.179 |
| Mean body wt. gms | 81.8 | 80.8 | 133.6* | 80.0 |

* high mean weight is in part caused by pregnant females.

or feeding side by side along fencerows. Virtually every standing piece of herbaceous vegetation had been consumed and cover was non-existent. Even in such conditions of density and lack of cover, all animals appeared to be in excellent condition, and with the coming of the spring, all females examined were pregnant with an average embryo count of 7.0.

Although *Sigmodon* is a very different animal from *Oryzomys,* adrenal responses to high density and the attendant effects should be manifest in both forms. If such comparative data is not in agreement one should look for other factors that may account for the rise and fall of populations.

Rather than postulating an indirect effect of climate and food upon the populations through social stress, we postulate a direct response of the populations to environmental vicissitudes via their reproductive physiology. This, in fact, seems more reasonable, in view of the general response of all rodents during the winter of 1957-58. We emphasize that social stress is not the only factor that may account for adrenocortical hypertrophy. We can say with assurance that mammals may become stressed by means entirely independent of social stress, *i.e.* starvation, temperature, etc. The response of the individual to the impact of these extrinsic variables is direct, based on experimental data now available (Dale, 1955; Ershoff, 1952; Selye, 1946). In fact, direct response to climate and food offers a more plausible explanation of some populations prospering at extremely high densities (Kalela 1949, Bodenheimer 1957, Elton 1942) than does the concept of social stress.

The adreno-pituitary hypothesis states that, "the growth of mammalian populations is controlled by a sociopsychological-physiological feed-back system that responds to changes in population density." (Christian, 1959b). We find this hypothesis difficult to accept as an explanation for our observations of *Oryzomys* and as a general statement about all mammals because of the following questionable aspects of the concept.

1. *Christian's experiments dealing with crowded mice in small cages served to simulate an isolated factor, density, which presumably affects the rise and fall of natural populations.*

The data of Crowcroft and Rowe (1957, 1958) cast doubt upon the utility of laboratory findings on crowded mice. They found significant infant mortality resulting from the observer's disturbance. Infant mortality has been one of the limiting factors in caged studies (Christian, 1956a). Pen size and nest box design also contributed to limitation of population growth. "Deaths of unweaned mice are more likely to be caused by intraspecific strife when the nest boxes are small, with a single opening than when they are large with a 'through passage'." "If such mechanisms of population control are so dependent upon specific experimental conditions, we must question their importance in free living populations." Some of Christian's experiments involved densities approaching one million per acre and more

—a magnitude never realized in nature. Hall (1927) recorded the highest density at 82,280 per acre in a plague of house mice and voles in California. Clarke (1955) failed to produce a decline in numbers in outdoor enclosures despite overcrowding, and yet intraspecific strife was certainly limiting their increase.

2. *The social stress theory has been applied to all small mammal populations and clearly requires some dependence upon density. It assumes that social interaction increases with density.*

Pearson (1960) studied a population of *Microtus montanus* as it increased 5 to 10 fold. The amount of photographically recorded activity in the runways and thus the social contact remained constant. Our studies of this same species in Wyoming corroborate Pearson's observations.

In the summer of 1960, following a sharp decline in small mammal populations, we found single pairs of adult *Microtus montanus* living in widely separated lush clumps of bluegrass (*Poa*). These animals had obviously overwintered. As their numbers increased through the breeding season, the young of several generations remained in the immediate area of the parents, but the network of runways increased with density. This colonial habit of *Microtus* families and the expansion of runway systems in the colony suggest to us that social contact does, in fact, remain quite constant. Presumably, as densities continue to rise, the colonial runway systems would continue to expand into the extensive uninhabited parts of the surrounding habitat. Social contact, however would remain constant, as shown by Pearson's data. Admittedly, densities and the network of runways may ultimately increase to levels which cause increased social contact. Many populations, however, decline when densities are far below those required to occupy all available habitat.

3. *Adrenal weight increase is a reflection of stress induced by increasing density or environmental factors mediated through the single pathway of social interaction.*

McKeever (1959) found no significant differences between mean adrenal weights of *Microtus montanus* from two high and five low density populations when animals of the same sex and reproductive condition were compared. During the reproductive season, weights of adrenals clearly differed between the sexes and depended on the reproductive condition of the animals. Reproductive activity resulted in small male adrenals and large female adrenals and the opposite situation existed in nonactive individuals. Pregnant females did not have larger adrenals than those which exhibited other conditions of sexual activity. McKeever suggested that "stress through malnutrition would result in a significant increase in adrenal size in males, but a decrease of even greater proportions in the adrenal size of females."

Southwick (1958) was unable to detect changes in reproduction, mortality, fecundity, or adrenal weights related to increasing density of house mice in English corn ricks, although 45% of the adult males showed signs of severe fighting. Southwick and Bland (1959) repeated Christian's experiments with caged mice of a different strain. They failed to detect changes in adrenal weights due to crowding.

Our *Sigmodon* adrenal weight data (Table 6) agree well with McKeever's observations. Male weights decreased with onset of reproductive activity, while female adrenals gained considerably in weight with increased reproductive activity. Louch (1958) also observed that reproductively active female *Microtus pennsylvanicus* had larger adrenals than males.

Thus in *Microtus montanus*, *Microtus pennsylvanicus*, *Sigmodon hispidus* and *Oryzomys palustris* the change in adrenal weight appears to be at least as much a reflection of reproductive influences as an index to a "sociopsychological-physiological feed-back system". Certainly both factors need to be taken into account. If more were known about the age composition and the reproductive condition of Christian and Davis' Baltimore rat studies, an explanation might be forthcoming for the high male adrenal weights and low female adrenal weights in the low stationary population.

4. *During peak populations fecundity drops as a result of increased social strife.*

Hamilton (1937) described high fecundity in the fall during a peak population and a drop in the proportion of pregnancies during the winter. Reproductive failure might more reasonably be attributed to the stress of cold weather.

Crowcroft and Rowe (1958) pointed out that "lowered fecundity in response to high numbers has not been found in any naturally occurring house mouse population."

5. *Nutrition and other environmental variables play a subordinate role to social stress and are simply fed into the "feedback system" through the single pathway, social stress.*

Quality of food has been virtually ignored in most of the work directed at demonstrating the importance of density dependent factors.

Poole's studies (1960) of the European hare, *Oryctolagus,* in Australia, substantiated Siivonen's (1957) suggestion that food quality may be of major importance in influencing fecundity, and thus population growth. Poole found that reproduction is a direct reflection of seasonal conditions, the onset of breeding being determined primarily by the occurrence of a flush of new pasture growth "in those years and areas where the 'autumn break', with its sudden amelioration of conditions, (rain followed by new pasture growth) is well defined, the autumn reproduction may have a sharp onset and reach a peak of density comparable with the spring activity."

Poole recorded 7 percent of the females pregnant in August preceded by 18 months of drought with but 0.80 inches of rain in July and 0.22 inches in the first two weeks of August. The pasture was dry. Further rain in September improved the pasture considerably and incidence of pregnancies rose to 78 percent. October rains were sparse, 0.03 inches, and the pregnancies dropped to 47 percent. Rains from mid October to the third week in November further increased pasture growth, and by November 15, 85 percent of the females were pregnant. Temperatures increased from a monthly maximum mean of 61°F in October to 79°F in December and about 80°F until February 1955. By early January 1955, pregnancies dropped to 9 percent.

Siivonen compared the peaks and troughs of a small herbivorous mammal (voles) and tetraonid populations over a 25-year period and found that they closely coincide. The low years were all preceded by late springs and the highs preceded by favorable springs, with respect to green plant food. Andersen (1952) found that the numbers of hares in Denmark rose and fell coincident with early and late spring over a 30-year period.

Siivonen noted that the "condition of the female during pregnancy and the suckling period of the first litter is reflected in the succeeding litters. If the first litter is not belated and if it is a success, this litter will usually be capable of reproduction during the same reproductive season." "The reproductive rate of the snowshoe hare in pens of Evo Game Research Station would seem to support this assumption. In years when the early spring plants have been largely delayed, the litters have in general remained small and their number per female has often been reduced to one only." By considering the severe spring of 1957, severest compared with the previous 12 years "as regards green plants," Siivonen was able to predict the decrease year in the capercaillie.

The 1958 *Sigmodon* plague that we observed in Texas was preceded by two springs of high rainfall and luxuriant plant growth, following a 7-year drought. Similar climatic circumstances led up to the plague populations of *Microtus montanus* in northwestern United States in 1958 (Vertrees, 1959).

The highest crude protein, carbohydrate, and mineral contents in grasses occur in the young actively growing stage and the level of these substances decreases with maturity. Rainfall leads to an increase in these nutrients (French, 1959).

Another important constituent of pasture grasses and other species is the plant estrogens. At least five types of estrogens are contained in over 50 species of plants representing numerous families (Andrews, 1958; Bradbury and White, 1954). At least three of the species are known to be preferred foods of certain mice; alfalfa in *Microtus ochrogaster* (Jameson, 1947) and *Poa* in *Microtus montanus* (Unpublished).

Jameson (1947) demonstrated the preference of *Microtus* for alfalfa (73 percent of cuttings in runways) where it constituted but 25 percent of the vegetation. During the 1957-58 plague of *Microtus* which swept the northwestern United States, the mice severely damaged red clover, alfalfa, potatoes, wild cherry, and wild plum, all of which contain estrogens. The estrogenic activity in alfalfa has great variability as to season, stage of maturity, time of year, lo-

cation of stand and the variety of alfalfa (Bickoff, 1959). High levels of estrogen are particularly evident however during early spring growth (Bullough, 1955). The levels also vary from one year to another (Bickoff, et al, 1960). Assay methods for the activity of plant estrogens demonstrate an increase in uterine weight, and ovulation may be induced in hares by injecting an extract of alfalfa.

The proximity of the primary consumers (herbivorous species) to the primary producers (green plants) would manifest great changes in reproduction if slight nutritional changes in the green food occurred. Our most drastically fluctuating animals (microtine rodents, hares, and tetraonids) are primarily dependent upon plant food whose nutritional levels are probably related to climatic changes.

In light of our present knowledge of nutritional changes in rodent plant foods (proteins, carbohydrates, minerals, and estrogens), a sharp change in the quality of green plants could have immediate effects on the reproductive potential and eventual influence on the rise or fall of the population.

Our model for population dynamics of *Oryzomys* leaves nutritional factors in a questionable state. Our data are presently lacking in this regard. Nevertheless, if as we suppose, plant nutrient levels are closely related to climatic events, then the population changes of *Oryzomys* on Breton Island do not contradict a climatic-nutritional hypothesis.

## VI. Summary

A rice rat population was studied for 3 years on Breton Island, Louisiana. The rat population was limited primarily to a *Fimbristylis* community on the south side of the island.

Decreases in density seemed to be closely related to severity and duration of winter. Densities were quite high in summer and fall of 1957, declined sharply in late winter of 1957-58, recovered gradually through the summer, fall, and winter of 1958, and into the summer of 1959. Another sharp decline occurred early in 1960. The winters of 1957 and 1959 were unusually severe.

Home ranges for many adult animals remained relatively stable for some months. The average home range size of males was somewhat larger than that of females.

The extent and time of the breeding season was variable. The rats ceased breeding in November, 1957, and did not begin again until the following May. Conversely, in 1958 breeding continued through the summer, fall, and winter, and into the spring and summer of 1959.

The average number of embryos per female in 1957 was 3.7, while for 1958-59 it was 6.0. The mean embryo count for all females was 4.8. On the basis of ovarian analysis, litter size appears to be influenced primarily by the number of ova released.

Trapping records indicate the average longevity of rice rats on Breton Island to be about 7 months. A few individuals live longer than one year.

A growth curve based primarily upon data from 49 known-age rice rats in the laboratory is presented. Apparently *Oryzomys* grow continuously for at least one year, which is longer than most individuals live in their natural habitat. Males and females become sexually mature at 40-45 days of age. Total length is a more reliable criterion of age than weight or other standard external measurements.

Adrenal weights varied with density and season. They were highest during severe winter months when populations were relatively dense, and lowest during summer months regardless of density.

Food habits of rice rats on the island were variable. Food consisted mainly of seeds and vegetation during the growing season; insects and fungus (*Endogone*) became important items at other seasons.

Considerable weight loss throughout the population occurred in the harsh winter of 1957-58, suggesting that food shortage may have been acute.

The impact of climatic factors with a changing food supply and the unsheltered nature of the habitat may have exerted a decisive influence on reproduction and mortality.

The concept of a density-dependent socio-psychological-physiological feed-back system as a basic mechanism regulating growth of mammal populations is questioned in light of our investigations and those of other authors.

## VII. Acknowledgements

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## Abstract

A three year study of the rice rat, *Oryzomys palustris*, on Breton Island, Louisiana, is reported. Information is recorded on population density changes, home ranges, reproduction, food habits, growth, adrenal weights, and behavior. Climatic and nutritional factors are considered of great importance in regulating population growth. The adrenopituitary hypothesis of Christian is discussed in light of these and other data.

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# TULANE STUDIES IN ZOOLOGY

Volume 8, Number 5 May 31, 1961

## A QUANTITATIVE STUDY OF THE MOVEMENT OF *PARAMECIUM CAUDATUM* AND *P. MULTIMICRONUCLEATUM*

D. F. SEARS,
*DEPARTMENT OF PHYSIOLOGY,*
and
LILA ELVEBACK,
*DEPARTMENT OF BIOSTATISTICS, SCHOOL OF MEDICINE, TULANE UNIVERSITY, NEW ORLEANS, LA.*

## NINE DIGENETIC TREMATODES OF MARINE FISHES FROM THE ATLANTIC COAST OF PANAMA

FRANKLIN SOGANDARES-BERNAL
and
LUCY McALISTER SOGANDARES,
*DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY, NEW ORLEANS, LOUISIANA*

TULANE UNIVERSITY
NEW ORLEANS

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# A QUANTITATIVE STUDY OF THE MOVEMENT OF *PARAMECIUM CAUDATUM* AND *P. MULTIMICRONUCLEATUM* [1]

D. F. SEARS,
*Department of Physiology,*
and
LILA ELVEBACK,
*Department of Biostatistics, School of Medicine,*
*Tulane University, New Orleans, La.*

A previous study of the effect of inert gases on oil-water emulsions suggested a mechanism whereby these gases could produce narcosis (Sears and Fenn, 1957). Extension of this research to a biological system was desirable. Reports that narcotics, *e.g.,* chloral hydrate, affected cilia and hence movement of paramecia (Alverdes, 1922) led us to investigate effects of pressures of inert gases on movement of these organisms. The theoretical work of Ludwig (1929) and the behavioral studies of Jennings (1923) presented factors involved in movement of paramecia. However, to use movement as a criterion of narcosis, these studies and others consulted did not yield sufficient quantitative information in the following aspects: (1) the three dimensional nature of the movement; (2) the basic measurements required to define the spiral path generated by the movement; (3) the most accurate method for estimating distances traveled; and, (4) whether measurements of movement of single paramecia or of groups would yield more reproducible data. Only by further characterization of paramecia movement was it possible to observe and quantitate narcotic action. This paper is a study of movement designed to supply the necessary quantitative information.

Data on speed were obtained from single individuals and groups of *Paramecium caudatum* and groups of *P. multimicronucleatum* under conditions which allowed description of typical speed, variability in speed during short time intervals, and change in mean speed over long periods of time. Individual differences among paramecia under the same experimental conditions were explored. Variations in measurements on single paramecia in a drop of media were compared with measurements in which the drop contained several paramecia. Data characterizing the spiral paths were obtained from experiments with *P. multimicronucleatum;* these data allowed us to test for a relationship between speed and shape of path. Finally, consideration was given to relative errors of one and two dimensional measurements of the three dimensional path.

*Methods and measurements.*—Hanging drop preparations of paramecia were used in most of the work. Pyrex discs were sufficient in size to permit observation of three drops during an experiment. Paths of free swimming paramecia were traced on paper using a *camera lucida* and timed with a stop watch. Lengths of these lines were determined with a map measurer. The length divided by the magnification gave an estimate of the distance traveled by the paramecium. A value for speed at a particular time represents a mean speed determined from at least five tracings of whatver paramecia appeared in the field during the two to three minutes usually required to make the tracings. Measurements were made alternately on the drops. Mean speed and standard deviation were calculated for each of these short periods of time. This procedure was used especially for measurements with single paramecia.

For comparison with these experiments, a chamber as designed by Ferguson (1957) was constructed. This stroboscopic dark field illumination method was used in experiments with *P. multimicronucleatum.* Paramecia paths were photographed and resulted in streaks on 35 mm film. The negatives were projected with a microfilm reader. A typical record for this type illumination is shown as figure 1. Due to the large num-

[1] This research was begun with funds supplied by Office of Naval Research Grant #NR-100-281 at the University of Rochester, Department of Physiology. Work with *P. multimicronucleatum* was supported by United States Public Health Service Grant #RG-5713, and carried out at Tulane University.

Figure 1. Photograph of paramecia paths with stroboscopic dark field illumination.

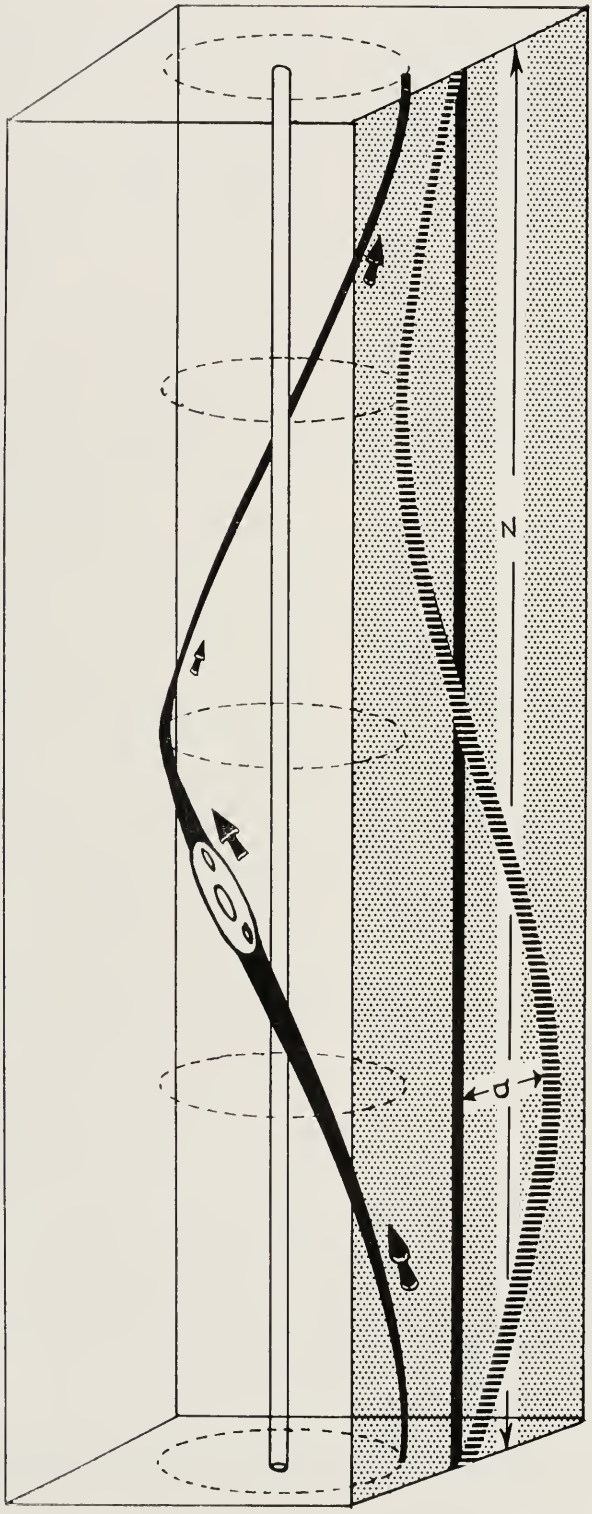


Figure 2. Schematic representation of the path of a paramecium. Measures of the length of one complete rotation, z, and the radius of the spiral, a, may be obtained from the two dimensional projection.

bers of measurements, the data were processed with the IBM 650 computer.[2]

*The shape of paramecia paths.*—The shape of a paramecium path has been described as helical (Ludwig, 1929). Determination of the three dimensional distance traveled may be derived from the parametric equation for a helix:

$$z = a\theta$$
$$x = a\cos\theta$$
$$y = a\sin\theta$$

As shown on figure 2, the width of the spiral is 2a, and the progression is assumed to be along the z axis of a Cartesian coordinate system. If $L_3$ represents the distance a paramecium travels in three dimensions for one complete rotation, *i.e.*, $\theta$ going from 0 to $2\pi$, then

$$L_3 = \sqrt{(2\pi a_0)^2 + z_0^2}$$

Obviously when $a = 0$, $L_3 = z$. Both z and a are available from sketches of paramecia paths or from photographs.

From these two measurements (z, a) the helix can be completely described. Thus the angle of progression ($\alpha$) is given by

$$\tan\alpha = \frac{z}{\theta a}$$

The tangent of this angle is the ratio of the distance along the major axis of the helix to the circumference of the cylinder about which the rotation occurs. The curvature K of the path at every point on the helix is

$$K = \frac{\cos^2\alpha}{a}$$

when $\alpha$ is 90°, cos $\alpha$ is 0 and the paramecium is swimming in a straight line. Torsion T in terms of $\alpha$ was given by Ludwig as:

$$T = \frac{\sin 2\alpha}{2a}$$

when the torsion is equal to curvature, the length of the spiral z is equal to the cylinder circumference about which the spiral is wound.

It has been reported (Walton, 1916, Ebbecke, 1935, and Sears, 1957) that rotation about the longitudinal axis of the organism or the curvature of the path changes under various conditions. This was the predominant effect determined for the response of paramecia to high pressures of argon (Sears, 1957).

*Errors in the measurement of distance.*—As already stated, we can calculate the three dimensional distance, $L_3$, by measuring the length of the major axis of the helix z and its radius a. Also it is possible to measure the distance $L_2$ with a map measurer following along the curve obtained from the tracing or photograph of the path. Finally z may be measured with a ruler.

In our early experiments we determined the $L_2$ distances and reported these in the majority of cases. $L_2$ measurements give more accurate results than straight line distances and allow easy estimates of rotation (see appendix). The availability of a computer made calculations of $L_3$ feasible in our recent experiments. The ratio of mean width to mean length of a spiral for *P. multimicronucleatum* was 0.041. Therefore the error as a proportion of $L_3$ when the distance is estimated by $L_2$ would be about one percent. However, the estimate obtained from *z* measurements would give a three percent error compared to $L_3$.

*Determination of speed.*—Primarily we sought to describe a pattern of movement of paramecia over time periods. There is possibility for variation in this pattern due to different experimental situations; differences in species, media, temperature, age, or pH. These sources of variation are fairly easily controlled. There are other variations, however, which are not amenable to external control. A simple paramecium will vary its speed during even short periods of observation. Therefore, it is desirable to report the mean and standard deviation of speed measurements for these short intervals of time. There is variation: (1) between speeds of single paramecia in the chamber at the same short time interval but in different drops; (2) in patterns of movement of two different paramecia over a long time interval; and, (3) variation between experiments (between single paramecia and between groups of paramecia). In an attempt to study external factors which might cause variability in speed, we measured speed of single individuals and groups of *P. caudatum* in tap water, lettuce media, malt media, and in a solution recommended by Chalkley (1930). This

[2] We are indebted to Mr. Bill Nettleton, Tulane Computer Center, for his assistance in programming and will gladly make this program available to any investigator.

solution contained NaCl (0.1 grams), $CaCl_2$ (0.006 grams), KCl (0.004 grams), $NaHCO_3$ (0.004 grams) in one liter of water.

*Basic variability.*—Figure 3 illustrates experimental data for single individuals of *P. caudatum*. One paramecium was placed in each of three hanging drops in the chamber. Four short interval sets of measurements were made on each drop. The five measurements made on each paramecium during each short interval are plotted, and we see that during a period of 2 minutes a paramecium may change its speed by a factor of two, although this is unusual. The extent to which the three paramecia differed in their pattern of speed with time is also illustrated. The set of data available for single *P. caudatum* was obtained from experiments in-

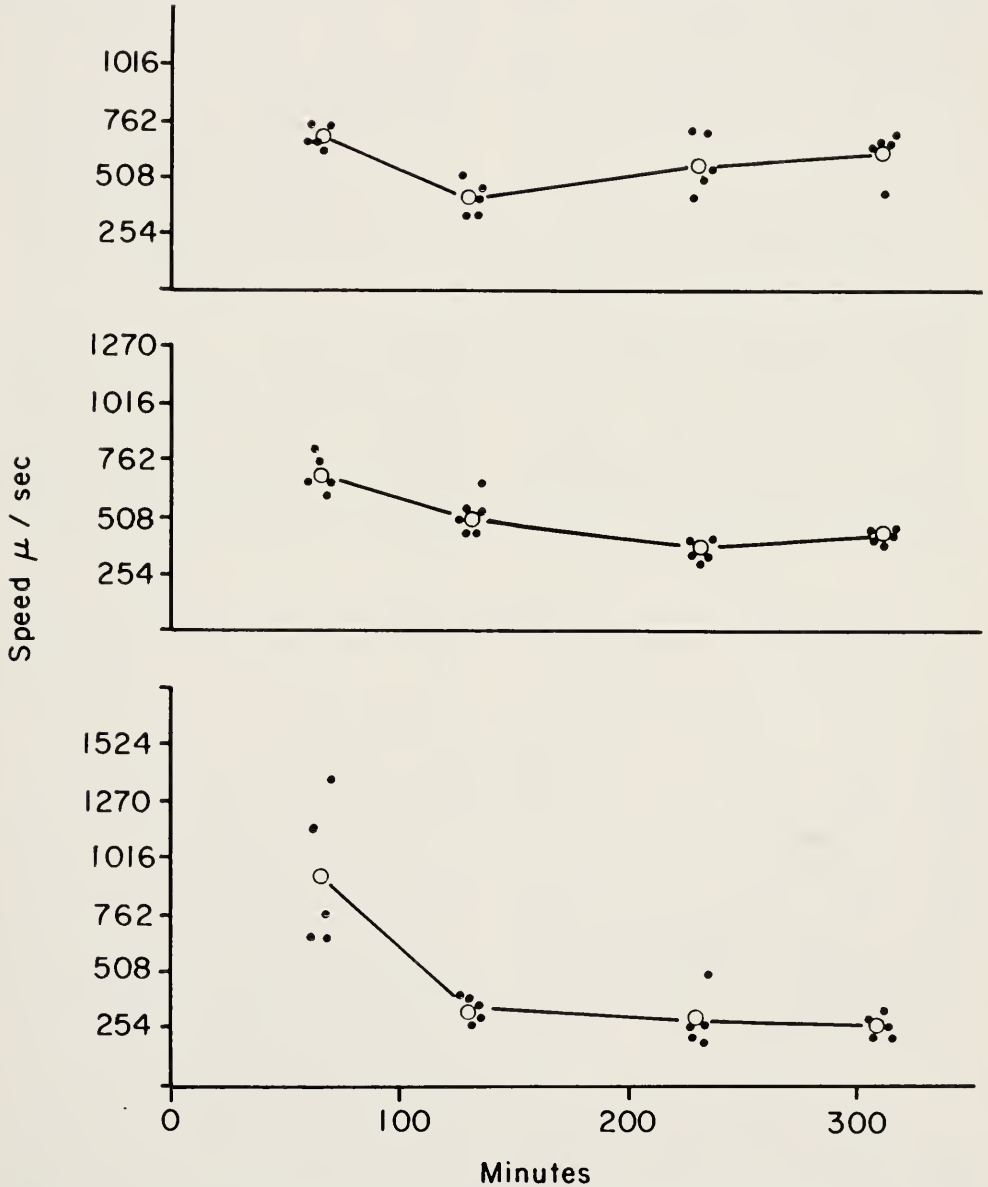


Figure 3. Variation in speed and mean speed of three single organisms (*P. caudatum*) in three different drops observed alternately. The small black dots represent single observations. Circles represent mean speed. (Note: 254 μ/sec = 0.01 inches/sec).

volving 80 drops each containing a single paramecium and involved a total of 219 sets of two or three minute intervals, taken from two minutes to 30 hours after the paramecia were placed in the chamber. The vast majority of measurement intervals were during the first 8 hours. Several media were used. Means and standard deviations of the five (or more) measurements made during the short intervals were studied.

*Speed of single P. caudatum.*—Standard deviations were computed for each of 219 two-to-three minute intervals, and differed greatly. Even within subgroups of the same media, temperature, pH, and time, differences corresponding to a factor of ten were observed. Distributions of these short interval standard deviations for Chalkley and other media (malt, lettuce, and tap water suspensions of paramecia) are illustrated in figure 4. Shown also are distributions of short interval standard deviations for drops containing more than a single paramecium. With several paramecia in the drop, standard deviations were only slightly larger than those for measurements made on single organisms. *With respect to speed measurements little is to be gained by limiting experiments to a single organism per drop.*

*Speed of P. caudatum and P. multimicronucleatum.*—In general, speed of both species decreases from the beginning of experiments but tends to approach equilibrium by the end of the third hour (fig. 5). This equilibration time seems to be characteristic of hanging drop preparations. Ferguson (1957) did not report any such long equilibration required to attain a mean speed when his chamber is used, and our experiments with his chamber bear this out. We suspect that variation in $CO_2$ tension of the drop makes equilibration necessary; we are now investigating this possibility.

Speeds measured in all experiments on both single or many organisms in a drop were averaged for each 100 minute interval. The time interval extends to 700 minutes. Scattered measurements at more than 2,000 minutes confirm the tendency to an equilibrium speed reached after about 300 minutes. Initial high mean speeds were frequently accompanied by large standard deviations.

The relationship between short interval means and standard deviation was examined graphically. For mean speeds in excess of 900 microns per second the standard deviations were, in the large majority of cases, also large. For moderate speeds, typical after three hours (254 to 635 $\mu$/sec), no relation-

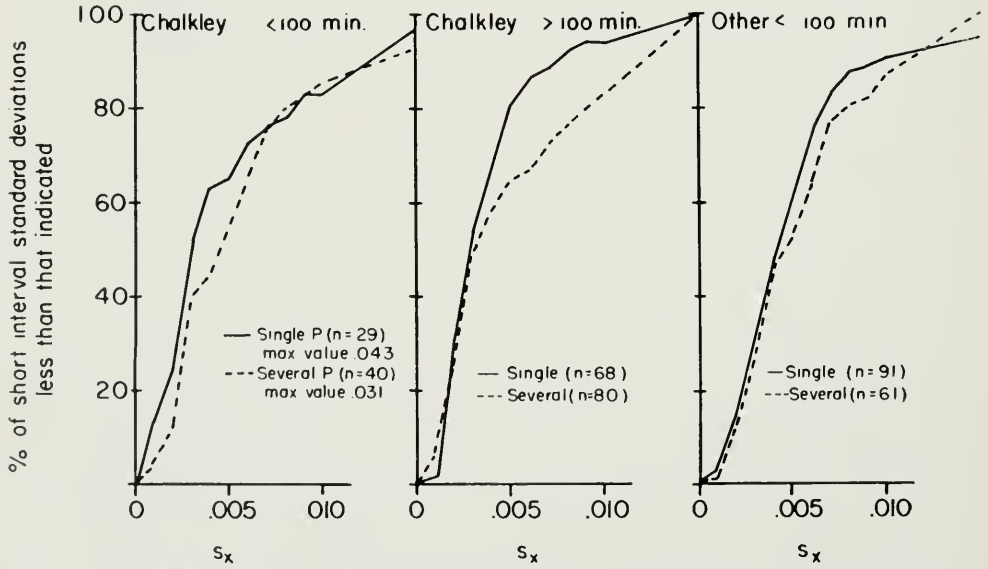


Figure 4. Standard deviations of measurements of short intervals speed grouped according to observations on single and many paramecia in a drop and in different media. Other media include tap water, lettuce media, and malt media. The values for standard deviation are in inches per second and must be multiplied by 25,400 to convert into $\mu$/sec.

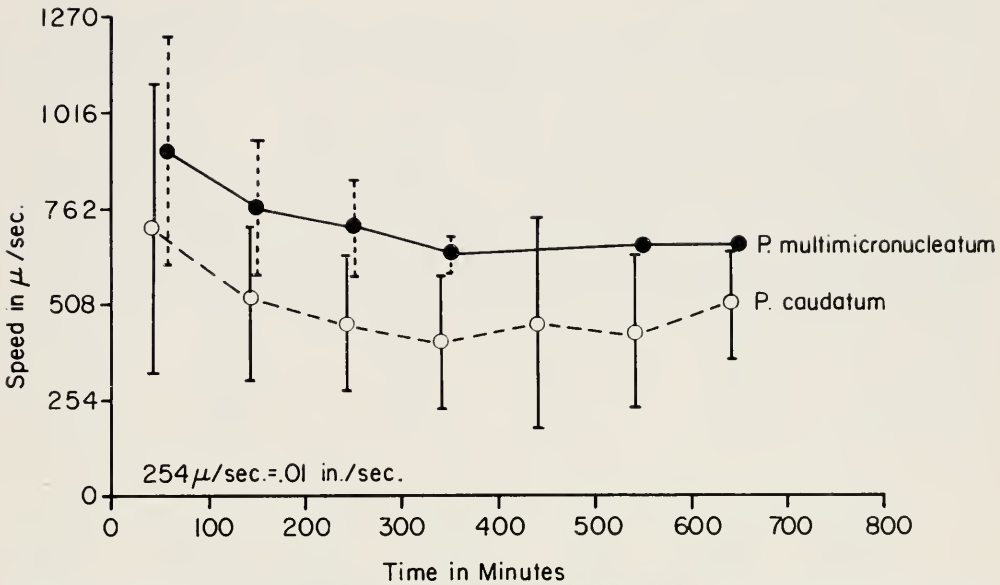


Figure 5. Speed of *P. caudatum* and *P. multimicronucleatum*. Bars through each point indicate standard deviations rather than standard errors of the mean since the great variability in speeds is of fundamental interest. Circles refer to *P. caudatum* and dots show mean speed for *P. multimicronucleatum*.

ship between short interval mean and standard deviation was detected.

Ferguson (1957) reported that thirty measurements are required for computation of a mean average velocity. From our measurements we estimate that mean speed of *P. caudatum* at 500 μ/sec with a standard deviation of 127 μ/sec. At least 70 speed measurements are required to reduce the error of the mean to three percent, and 625 are required for a one percent error. Thirty measurements lead to nearly 5% error of the mean from these values. This may be another difference in hanging drop preparations and the closed Ferguson chamber.

*Characteristics of the path of P. multimicronucleatum.*—From photographic tracings we were able to measure length z as the distance from one peak to the next, and width a as half the depth of the valley of the track, (see fig. 1). We analyzed the length and width of the spiral only for *P. multimicronucleatum*. There were many paramecia in each drop under observation. Photographic tracings of movement were measured at 173 × magnification. Length and width of one complete spiral turn were studied in relation to corresponding speed. The data covered a wide time interval and several temperatures. The greatest number of measurements were made at 20° C. As many as 10 measurements of the spiral were obtained at each short time interval. Measurements of a, z and speed were made on a total of 334 paths.

The set of 334 paths studied were first ordered on speed. In studying change in the mean values of a and z with speed, speeds were grouped in intervals of 130 μ/sec (0.005 inches/sec). Means are plotted in figure 6. Of the three variables, a, z, and speed, the diameter of the spiral, a, had much the largest relative variability. Part of this effect may be due to the fact that, in relative terms, measurement error in a was larger than in z or in speed. It will be seen from figure 6 that there was little change in average length or width of the spiral over the speed range. If a relationship exists it would be a tendency for z to increase with speed.

The relationship of a to z was examined by plotting (a, z) pairs for paths corresponding to the 120 lowest speeds (281 to 635 μ/sec) and for the 120 highest speeds (889 to 1651 μ/sec) (fig. 7). In each of the two groups correlation between a and z

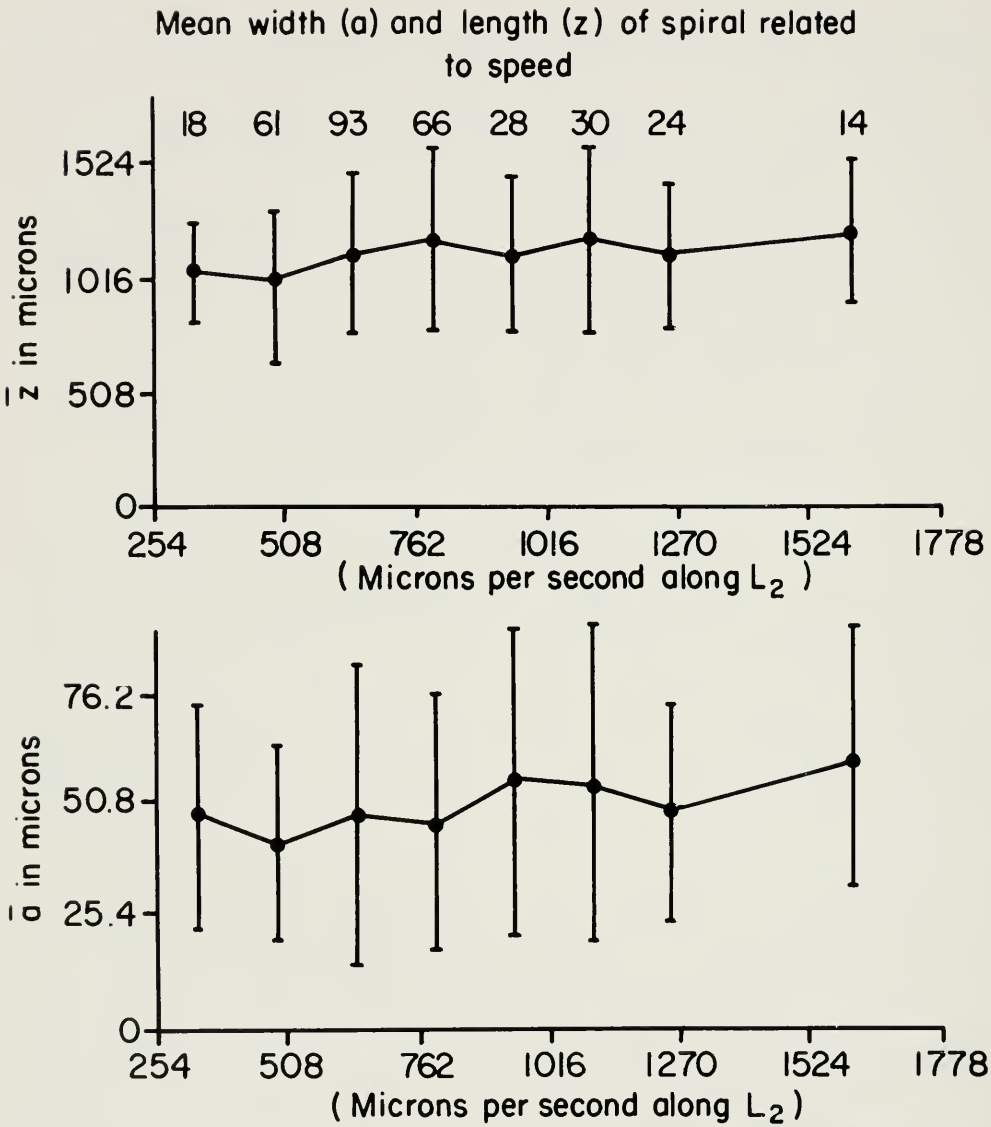


Figure 6. Mean width a and length z of the spiral of *P. multimicronucleatum* related speed. At the top of the figure are the numbers of obseravtions for each speed grouping.

was weak but positive. There was some tendency for large values of a and z to occur together, and this tendency was stronger at high speeds than low.

Sets of measurements made on the same drop during a short period of time were also studied. Short intervals means ($\bar{a}$, $\bar{z}$) were plotted against each other. Again positive, but weak, correlation was observed. The times covered ranged from 5 to 422 minutes after paramecia had been put into the chamber. These times seemed to bear no relation whatever to $\bar{a}$ or $\bar{z}$ values.

From experiments carried out at 20° C, four short interval sets of measurements made during the first hour after putting paramecia into the chamber were analyzed, and compared with four short-interval sets of measurements made after 172 minutes. Coefficients of variation were as follows:

| Time (in minutes) | 5 | 7 | 43 | 45 | 172 | 233 | 289 | 388 |
|---|---|---|---|---|---|---|---|---|
| No. measurements | 9 | 12 | 6 | 19 | 12 | 10 | 5 | 10 |
| Coeff. of Var. | | | | | | | | |
| z | 35 | 20 | 12 | 29 | 29 | 37 | 23 | 30 |
| a | 50 | 39 | 41 | 53 | 44 | 69 | 70 | 49 |
| speed | 47 | 16 | 21 | 27 | 21 | 22 | 21 | 22 |

Data presented here were characterized by great variability in a and z even in the same drop during a short period of time. For example at 20° C and 289 minutes after paramecia were placed in the chamber five paths gave the following measurements:

| Speed ($\mu$/sec) | z ($\mu$) | a ($\mu$) | $\alpha$ | Curvature K ($\mu^{-1}$) | Torsion T ($\mu^{-1}$) |
|---|---|---|---|---|---|
| 584 | 1097 | 116 | 56° | 0.0026 | .0040 |
| 279 | 810 | 29 | 77° | 0.0017 | .0076 |
| 610 | 1128 | 58 | 72° | 0.0017 | .0051 |
| 356 | 1504 | 116 | 64° | 0.0017 | .0034 |
| 610 | 1011 | 17 | 84° | 0.0059 | .0062 |

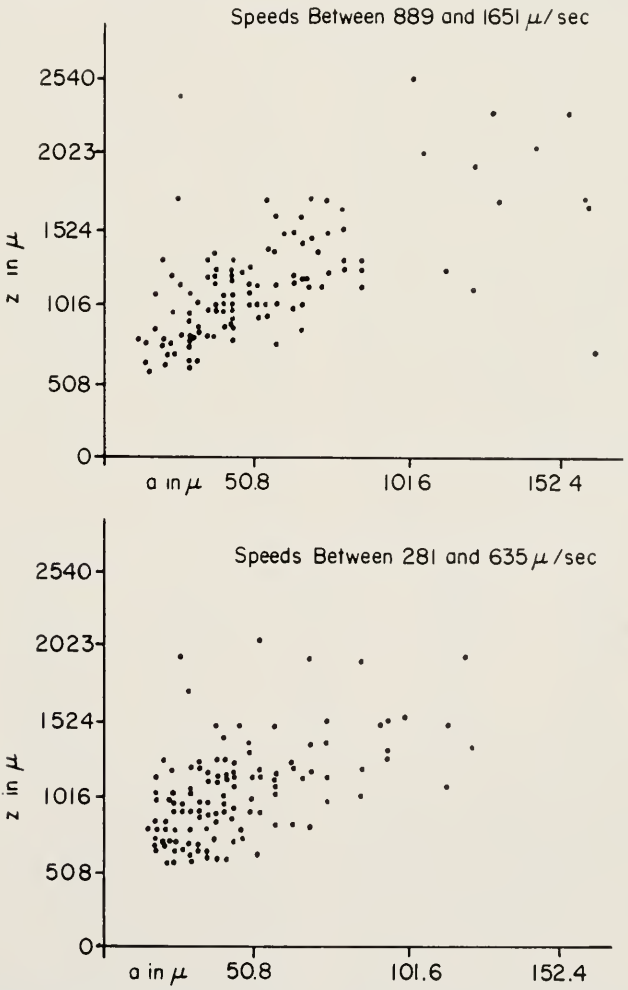


Figure 7. Relation between length of spiral z and width of that spiral a. Upper plot of distance related to the ratio of a to z.

Since there were many (perhaps 10 to 12) paramecia in each drop studied, we cannot, on the basis of these data, say what part of the variability observed is a reflection of difference between paramecia. We have only begun to study the variability in spiral shapes of single paramecia.

*An interpretation of the spiral movement.*—A theoretical study of spiral movement of ciliates was reported by Ludwig. He stated that two forces are responsible for the spiral path: one, a force which alone would cause the organism to go in a circle; the other, a force which causes the organism to rotate about its longitudinal axis. A canoe, if paddled on one side more strongly than the other, will travel in a circle with the side having the greatest force applied directed outward. Ludwig stated that force exerted by cilia of paramecia on the aboral side normally exceeds that applied by the oral side. This causes the organism to make a basic circle. There is a rotation component to the force which cilia are supplying which causes the organism to rotate about its longitudinal axis. This rotatory movement has been attributed to the oblique direction of the cilia beat from left backward, toward the right.

The organism, therefore, may start moving in a circle to the right, but due to accompanying rotation of the organism, the circle changes to be directed upward, then to the left, downward, and finally to the right again. Thus, a spiral results.

Ludwig stated that characteristics of the spiral are affected by changes in curvature (arising from differences in force applied on the oral and aboral surfaces) and changes in torsion (arising from differences in direction of cilia beat). Consideration of these changes led him to three generalizations:

(1) If the curvature remains constant, increasing torsion (rotation) would result in a steeper and more narrow spiral. (That is, a large value for z and smaller for a).

(2) If the torsion remains constant but the curvature increases, the spiral line becomes fatter (z would decrease) and the width a would increase until the paramecium makes an angle of 45° with the XY plane (assuming progression along the Z axis). As the angle decreases toward zero, the width of the spiral would then decrease.

(3) Asymmetry in rotatory force components causes a widening and flattening of the spiral path.

Ludwig (1929) and Bullington (1925) attempted to determine whether characteristics of spiral patterns would aid in classification of ciliates. Bullington concluded that among species "speed of swimming is directly related with the number of spiral turns. Increasing the speed increases the length of the spiral". It was this statement and the first rule of Ludwig's which caused us to investigate whether, in order to increase their speed, paramecia of the same species alter the spiral paths which they follow.

Three values for curvatures given above are constant (0.0017 $\mu^{-1}$). The torsion changes and in this case, in agreement with Ludwig's generalization, the radius, *a*, varied inversely with the torsion; the length of the spiral increased. The question arises to what extent a single paramecium can produce these changes. The following values were obtained from a single *P. multimicronucleatum* in a hanging drop:

| Minutes | Speed | z | a | *a* | Curvature K ($\mu^{-1}$) | Torsion T ($\mu^{-1}$) |
|---|---|---|---|---|---|---|
| 20 | 600 | 1300 | 38 | 80° | 0.0009 | 0.0045 |
| 20 | 1000 | 1850 | 145 | 64° | 0.0013 | 0.0027 |
| 20 | 900 | 1330 | 72 | 71° | 0.0014 | 0.0043 |
| 20 | 1500 | 1965 | 214 | 56° | 0.0015 | 0.0022 |
| 78 | 900 | 1156 | 58 | 73° | 0.0016 | 0.0048 |
| 157 | 400 | 1450 | 72 | 73° | 0.0013 | 0.0039 |
| 221 | 700 | 1127 | 43 | 77° | 0.0012 | 0.0051 |
| 221 | 600 | 1272 | 72 | 70° | 0.0016 | 0.0044 |
| 392 | 300 | 867 | 101 | 54° | 0.0034 | 0.0047 |

Characteristics of the rotation could be measured from only about a fourth of the photographs of the paths. In many cases the paramecium swam in a straight or nearly straight line. Although rotation about the longitudinal axis occurred, no radius, *a*, could be measured. Where measurable rotation occurred the curvature remained fairly constant. Since curvature is related to the bal-

ance of forces on the oral and aboral sides, we may conclude that this ratio of forces was generally maintained. The torsion indicates the variation in direction of the cilia beat. There is a weak relationship obtainable from the extremes of the speeds that indicates that the length of the spiral increases with increase in speed. However, the middle speed values do not show any clear evidence for such a relationship.

As we have shown, there is much variation in the shape of paths which paramecia follow. However, our mean path length and width agree closely with those found by Bullington for *P. multimicronucleatum.*

paths of paramecia is illustrated in the following data (25° C).

| Experiments | No. of z measurements | z (μ) |
|---|---|---|
| Control (1) | 403 | 1607± 51 |
| Control (2) | 186 | 1543± 30 |
| Added $CO_2$ (1) | 218 | 1688± 94 |
| Added $CO_2$ (2) | 82 | 1673± 86 |
| Ethyl alcohol 2.58 | 43 | 2267±157 |

Mean z values for *P. multimicronucleatum* placed in the Ferguson chamber in the culture media differ little (about 3%) between the two experiments. Bubbling 100 percent

| Reference | Mean z | Range | Mean a | Range |
|---|---|---|---|---|
| Bullington, 1925 | 1290μ | 833-1666μ | — | 143-200μ |
| Our data | 1121μ | 402-2540μ | 46μ | 11.5-162μ |

We also measured the length along $L_2$ corresponding to a single rotation for *P. caudatum.* The mean length of the spiral path of this species so measured (not calculated from z and a is 784μ. We did not measure widths of paths. Bullington's value for length of the spiral of *P. caudatum* were from 900 to 2250 microns.

Results presented are for many different paramecia and do not show what happens to an individual path as a paramecium increases its speed. (See fig. 6) But we expected that in the study of 334 paths any decided tendency to change either length or width of spiral with increasing speed would have been discernible. We can only say that in the hanging drop preparation the tendency for length of the spiral to increase with speed is weak but if a real relationship exists it is indeed that both increase together.

Again there was a difference in the values obtained depending upon the nature of the preparation. The mean z values reported above from our studies were taken from the hanging drop preparation. Using the Ferguson chamber where the paramecium's path is not restricted to the diameter of a drop, the mean z is greater, about 1660μ. Using the data obtained from this chamber we plotted the mean lengths of rotations z against speed and found an indication that speed and length of rotation increase together. However, the scatter was great.

The use of z to indicate changes in the $CO_2$ in the media caused no significant change. However 2.58 volumes percent ethyl alcohol produced a significant change. This amount of alcohol was not lethal to the paramecia.

Four concentrations of $CO_2$ were used: 10%, 50%, 90% and 100% of one atmosphere. The mean z values with added $CO_2$ were little different from experiments with adding $CO_2$. However, the mean a value for the experiments with $CO_2$ (300 measurements) was 126 μ compared to 195 μ where $CO_2$ was not artificially raised. The lowest a values were associated with the 90 percent $CO_2$ experiments. With no essential variation in z this indicates a straightening of the paramecia paths as the concentration of $CO_2$ increased. We therefore propose the use of orientation (the angle $\alpha$) to indicate a positive attraction to the gradient of a chemical.

*Experimental design.*—Relating this investigation to experimental design, we find little difference in basic variability of speed measurements whether observations are made at controlled temperatures in lettuce media, malt media, tap water, or a salt solution at pH 6.8. Observations on single paramecia gave smaller standard deviations, but the difference compared to observations made on groups of paramecia was small. Equilibration after the organisms were placed in the hanging drop, gave smaller standard deviations and also a more stable mean speed.

The mean speeds obtained here agree closely with those obtained by other investigators and lend support to the use of the change in mean speed as an index of response in certain experimental situations. However, complete characterization of the spiral path is desirable to give information about the force and direction of the cilia activity.

## Summary

(1) Three measurements are necessary to characterize movement of a paramecium; length of the spiral, width of the spiral, and speed of the organism progressing along this path.

(2) Of the three methods of estimating the actual distance traveled by a paramecium per unit of time, calculating the three dimensional path length ($L_3$) is the most accurate. The distance measured along the two dimensional projection of the path may be expected to give an error of about 1% compared with $L_3$; the straight line distance underestimates $L_3$ by about 3%.

(3) Hanging drop preparations of paramecia are characterized by rapidly changing mean speeds during early periods after formation (time $<$ 180 minutes). After equilibration more stable mean speeds are obtained.

(4) The mean speed of *P. caudatum* at 25° is between 400 and 500 $\mu$/sec. For *P. multimicronucleatum* this mean is between 600 and 700 $\mu$/sec.

(5) Measurements of mean length and width of the spiral of *P. multimicronucleatum* in hanging drops give: length $z = 1121\ \mu$, width $a = 46\ \mu$.

(6) There is little advantage in measuring speed on many single paramecia individually as compared to groups.

## Appendix

### *Error Involved in Measurement of Distance*

The actual distance traveled by a paramecium may be calculated if one assumes that the organism swims along a perfect helix. There are two other measures of distance traveled which are considered less accurate estimates. One is the length of the curved two dimensional projection of the path, the other is the straight line distance from start to finish ($z$ on fig. 2).

The three dimensional distance traveled may be derived from the parametric equations for a helix:

$$z = a\,\theta$$
$$x = a\cos\theta$$
$$y = a\sin\theta$$

If $L_3$ is the arc length the paramecium travels during one complete rotation ($\theta$ doing from 0 to $2\pi$) then

$$L_3 = \sqrt{(2\pi a)^2 + z^2}$$

where a is the radius of the helix and z is the distance traveled in the direction of the major axis during one rotation.

If one measures the two dimensional projection of the path as shown in figure 2, the accuracy of this estimate is between z and $L_3$. Comparison of the length of the two dimensional path, $L_2$ with $L_3$ may be made by also determining this length from a and z as was done for $L_3$. If

$$b = \frac{z}{2\pi}$$

then the two dimensional arc length corresponding to one complete rotation, $L_2$ is given by

$$L_2 = \int_0^{2\pi} (b^2 + a^2\cos^2\theta)^{1/2} d\theta$$

$$= 4(a^2 + b^2)^{1/2} \int_0^{\pi/2} (1 - K^2\sin^2\theta)^{1/2} d\theta$$

where

$$K^2 = \frac{a^2}{a^2 + b^2}$$

Here the elliptical integral will not simplify therefore, it must be evaluated for each value of z and a from tables. (Mathematical Tables from the Handbook of Chemistry and Physics, Ed. 9, page 238.)

The relative errors, $\frac{L_3 - z}{L_3}$ and $\frac{L_3 - L_2}{L_3}$ can both be expressed as functions of the ratio a/z:

$$\frac{L_3 - z}{L_3} = 1 - ((2\pi a/z)^2 + 1)^{-1/2}$$

$$\frac{L_3 - L_2}{L_3} = 1 - (2/\pi)E$$

where E is

$$\int_0^{\pi/2} (1 - K^2\sin^2\theta)^{1/2} d\theta$$

These relative errors are shown graphically in figure 8.

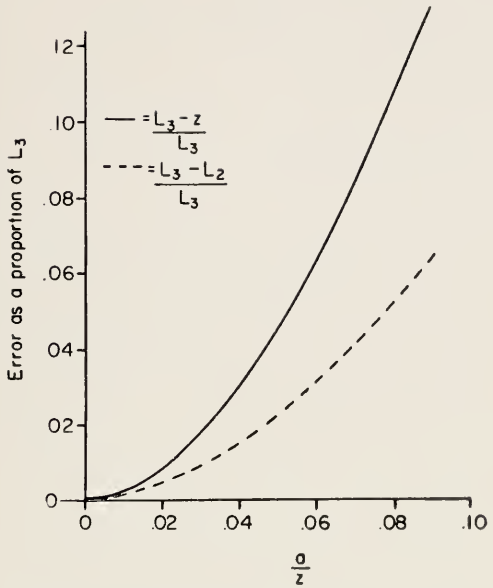


Figure 8. Magnitude of error is measure of distance related to the ratio of $a$ to $z$.

In data studied here the ratio a/z exceeded 0.06 for less than ten percent of the paths studied, and exceeded 0.07 in only four percent of these paths. This means the relative error in using distance along $L_2$ rather than along $L_3$ is small.

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## Abstract


The investigation reports experimental methods for determination of speed and rotation of paramecia. Three measures are necessary to characterize movements of paramecia: speed of the organism, and the length and width of the path along which movement is occurring. Mean speeds of *P. caudatum* at 25°C are between 400 and 500 microns per second (time>180 minutes). For *P. multimicronucleatum* these means are between 600 and 700 $\mu$/sec.

For *P. multimicronucleatum* the mean length of a complete rotation about the longitudinal axis is 1121 microns, the radius of the spiral 46 microns.

Several factors involved in the design of experiments on movement of paramecia were discussed.

# NINE DIGENETIC TREMATODES OF MARINE FISHES FROM THE ATLANTIC COAST OF PANAMA[1]

FRANKLIN SOGANDARES-BERNAL
and
LUCY McALISTER SOGANDARES,
*Department of Zoology, Tulane University, New Orleans, Louisiana*

Studies of the geographical distribution of marine Digenea in recent years have given rise to speculation regarding similarities of the trematode faunas from both American continental oceans. The first important studies attempting to explain the geographical distribution of American marine Digenea were by Manter (1934, 1940a, 1947, 1954, 1955). Several workers, mainly Hanson (1950), Siddiqi and Cable (1960), Sogandares (1959), Sparks (1957, 1958, 1960), and others, have also studied the geographical distribution of American marine trematodes. The area of the formerly submerged Isthmus of Panama, the most recent continuity between the American Atlantic and Pacific Oceans, has figured prominently in explanations regarding the similarities of the trematode faunas.

Previous collections of marine Digenea from Panama were made on the Pacific coast only. Almost the entire body of literature on Atlantic Digenea, on which comparisons with the Pacific Digenea are based, represents studies in coastal waters of Maine, Massachusetts, North Carolina, Florida, and Louisiana; and in the islands of Bermuda; Tortguas, Florida; Bimini and Nassau, Bahamas; and Puerto Rico. In view of the relatively recent connection of the two oceans at the Isthmus of Panama we made at least a preliminary sampling of the Digenea of the Atlantic coast in this area.

The following digenetic trematodes were collected from the Atlantic coast of Panama during August, 1960. Unless otherwise specified all measurements are in millimeters.

## *Family BUCEPHALIDAE*

### *Bucephaloides arcuatus* (Linton, 1900) Hopkins, 1954

(figs. 1 to 7)

*Host.*—*Sphyraena barracuda* (Walbaum); great barracuda; family Sphyraenidae.

*Incidence of infection.*—In 1 of 1 host.

*Location.*—Pyloric ceca.

*Locality.*—Colon Reef, Republic of Panama [new locality record].

*Discussion.*—Linton (1900) named and described *Gasterostomum arcuatum* from *Sarda sarda* (Bloch) in Woods Hole, Massachusetts. He also (1905) reported the species from *Scomberomorus regalis* (Bloch) in Beaufort, North Carolina. In another report Linton (1910) briefly described (pp. 80-81; figs. 223-225) three species under the name *Gasterostomum* sp. from the great barracuda in Tortugas, Florida. Manter (1940b) reported *Bucephalopsis arcuatus* (Linton, 1900) Eckmann, 1932 from *Sphyraena barracuda* in Tortguas, Florida, pointing out that Linton's (1910) *Gasterostomum* sp. from the barracuda was confused with at least two species, *Bucephalopsis longoviferus* Manter, 1940 and *Bucephalopsis arcuatus*. Linton (1910) had confused three species under the name *Gasterostomum* sp. His figures 223 and 224 respectively probably represent *Bucephaloides arcuatus* (Linton, 1900) Hopkins, 1954 and *Bucephaloides longoviferus* (Manter, 1940b) Hopkins, 1954, while his figure 225 is probably a species of *Bucephalus* Baer, 1826. In 1932 Eckmann transferred *Gasterostomum arcuatum* Linton, 1900 to the genus *Bucephalopsis* Diesing, 1855. Apparently unaware of Eckmann's (1932) combination, Linton (1940) subsequently reported *Gasterostomum arcuatum* from *Sarda sarda, Scomber scombrus* Linn., *Trichiurus lepturus* Linn., and *Gadus morrhua* Linn., in Woods Hole, Massachusetts. Hopkins (1954) reserved the genus *Bucephalopsis* for a larval bucephalid trematode, *Cercaria haimeana* La Caze-Duthiers, naming the genus *Bucephaloides* for all other species formerly in *Bucephalopsis*. Sogandares (1959) reported *Bucephaloides arcuatus* from *Sphyraena barracuda* in Bimini, Bahamas. Siddiqi and Cable (1960) reported *Bucephalopsis arcuatus* from the same host in Puerto Rico. Yama-

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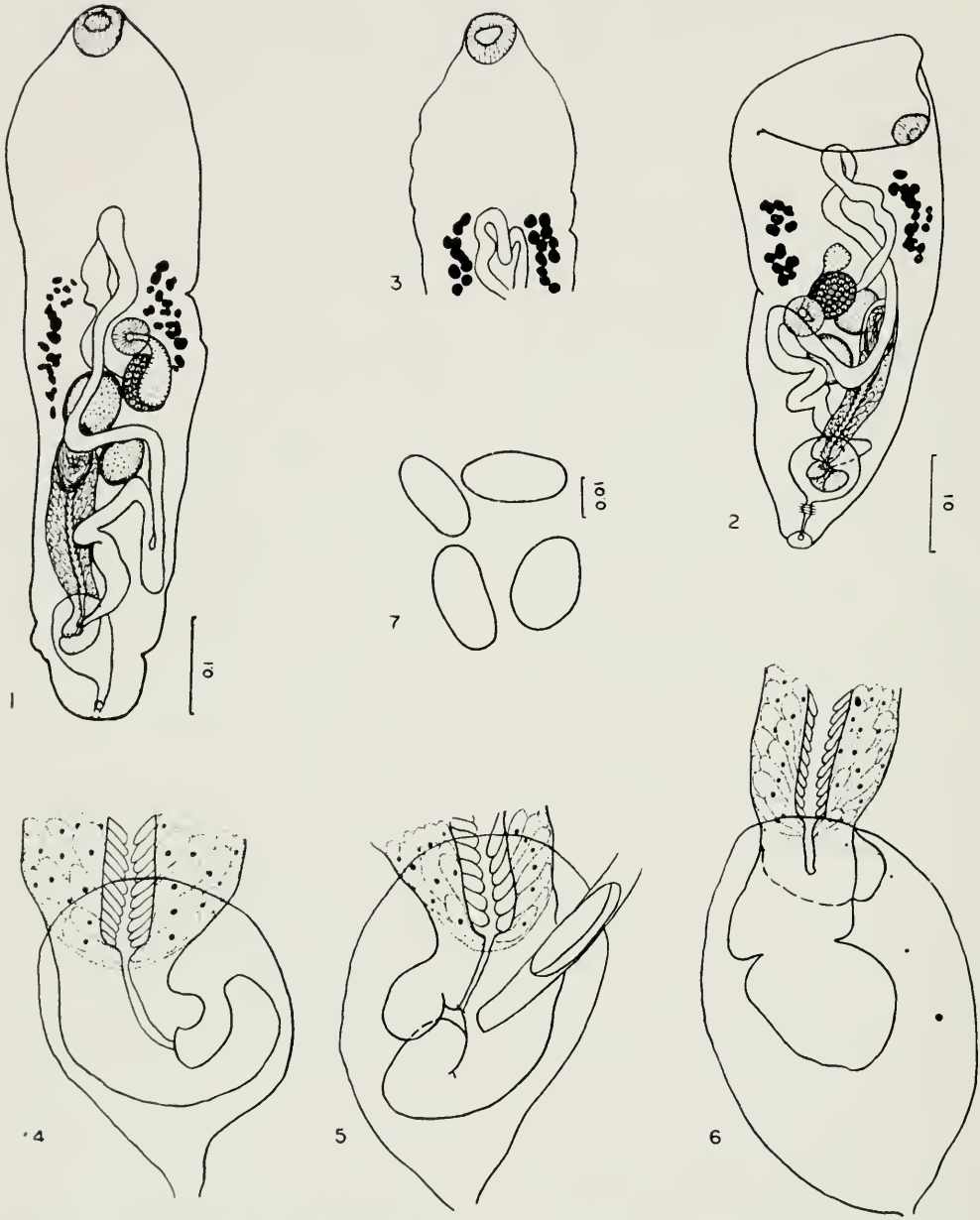



Figures 1-7. *Bucephaloides arcuatus*. **1, 2.** Dorsal and ventral views of whole mounts. **3.** Ventral view of anterior portion of forebody. **4, 5.** Central and dorsal views of genital atrium showing genital lobe and portion of cirrus sac. **6.** Dextrolateral view of genital atrium showing genital lobe and portion of cirrus sac. **7.** Uterine eggs. Unless otherwise specified, all figures were drawn with the aid of a Leitz camera lucida for inclined microscopes. The projected scale has the approximate value in millimeters.

guti (1958) regarded *Bucephaloides* a synonym of *Bucephalopsis*. Since we do not know into what genus *Cercaria haimeana* will develop, Hopkins' (1954) views will be followed until evidence proves otherwise.

The Panama specimens of *B. arcuatus* have eggs resembling those of *B. longoviferus*, most eggs (fig. 7) measuring from

26 to 29 by 9 microns. One egg (fig. 7) measured about 24 by 17 microns. The Panama specimens differ from *B. longoviferus* in details of the genital lobes (figs. 4-6) and a uterus that never extends posteriorly beyond the genital atrium (figs. 1, 2) or to the anterior sucker (figs. 1-3). The Panama specimens differ from Manter's (1940b) redescription of *B. arcuatus* mainly in egg size, in the more anterior extent of the uterus, and by possessing more vitelline follicles. Egg size is a variable character in certain bucephalids and cannot usually be relied upon to show species differences. The anterior extent of the uterus is sometimes a more reliable systematic character. The anterior uterine extent of our specimens (figs. 1-3) intergrades with Manter's (1940b) redescription of *B. arcuatus* and extends the range. The number of vitelline follicles is difficult to count in our material because we cannot be sure if what frequently appears to be a separate follicle overlapping another follicle, is in reality a single branched follicle, or one which is cytolized. Further study of live *B. arcuatus* from the Panama Atlantic and more northern waters may show that there are actually three species of *Bucephaloides* in *Sphyraena barracuda*. The present evidence seems to indicate that we are probably dealing with a different population of *B. arcuatus*.

*Family OPECOELIDAE*
*Subfamily Plagioporinae*
*Hamacreadium mutabile* Linton, 1910
(figs. 8 to 15)

*Host.*—*Ocyurus chrysurus* (Bloch); yellow-tail; family Lutjanidae.

*Incidence of infection.*—In 2 of 2 hosts.

*Location.*—Intestine.

*Locality.*—Galeta Point, Republic of Panama [new locality record].

*Discussion.*—*Hamacreadium mutabile* was reported from *Lutjanus griseus* (Linn.), *L. apodus* (Walbaum), and *Anisotremus virginicus* (Linn.) at Tortugas, Florida by Linton (1910). While at Tortugas, McCoy (1929, 1930) experimentally obtained adults of *H. mutabile* from *Lutjanus griseus* and *Ocyurus chrysurus*. Manter (1947) also reported the following additional hosts for *H. mutabile* at Tortugas: *Lutjanus jocu* (Bloch and Schneider), *L. analis* (Cuv. and Val.), and *L. synagris* (Linn.). In another paper Manter (1940c) reported *H. mutabile* from *Lutjanus viridis* (Val.) and ? *Mycteroperca xenarcha* Jordan in the Galapagos Islands. Sogandarés (1959) reported *H. mutabile* from *Epinephelus striatus* (Bloch), *Haemulon sciurus* (Shaw), *Lutjanus synagris*, and *Petrometopon cruentatus* (Lacépède) in Bimini, Bahamas. Siddiqi and Cable (1960) reported *H. mutabile* from *Lutjanus analis*, *L. jocu*, *L. griseus*, *L. apodus*, and *Ocyurus chrysurus* in Puerto Rico. They also described two new species, *Hamacreadium lintoni* from *Epinephelus striatus* and *Cephalopholis fulvus*, and *H. longisaccum* from *Epinephelus adscensionis* in Puerto Rico. The descriptions of *H. lintoni* and *H. longisaccum* both fall within the range of variation observed for *H. mutabile*. Furthermore, *H. mutabile* is known from *Epinephelus striatus* in Bimini, Bahamas. Nagaty (1941) reported *H. mutabile* from *Serranus merra* (Bloch) (= *Epinephelus merra*), *Lethrinus mahsena* Forsk., *L. nebulosus* Cuv. and Val., *Teuthis marmorata* Günther, and *Lutjanus fluviflamma* (Forsk.) (= *Diacope fluviflamma*) in the Red Sea. He also believed *Hamacreadium epinepheli* Yamaguti, 1934, from *Epinephelus akaara* Temm. and Schl. and *Lethrinus haematopterus* Temm. and Schl. in Japan, to be a synonym of *H. mutabile*.

*H. mutabile* has been reported from at least nineteen different host species of which about 42 percent are in the family Lutjanidae, 26 percent in the Serranidae, 15.7 percent in the Lethrinidae, 10.52 percent in the Pomadasyidae, and 5.25 percent in the Acanthuridae. The major host groups are the lutjanids, serranids and lethrinid fishes. The pomadasyids and acanthurids are possibly accidental hosts of *H. mutabile*, though the pomadasyids are related to the lutjanids, serranids and lethrinids.

Our specimens of *H. mutabile* have only slightly lobed or smooth testes and the ovaries are either smooth or deeply lobed (figs. 8-15). The cirrus sac does not overlap the acetabulum in one preadult (fig. 12) and usually comes into contact with or overlaps the acetabulum by about half its length in adults (figs. 8-10), and preadults (figs. 11, 13-14), extending to beyond the posterior border of the acetabulum in one adult contracted specimen (fig. 15). The genital pore position of our 12 *H. mutabile*

Figures 8-14. *Hamacreadium mutabile*. **8, 9.** Ventral views of whole mounts. **10.** Dorsal view of much contracted specimen. **11-14.** Ventral views of preadults showing variation in posterior extent of cirrus sac.

specimens is sinistral. The esophagus varies considerably in length, depending mainly upon the degree of contraction of the forebody (figs. 8-15). The vitellaria of our specimens are almost always confluent in the region of the cecal bifurcation. The excretory vesicle usually extends to the cecal bifurcation.

Yamaguti (1958) lumped several families of trematodes under the name Allocreadiidae. We are not following Yamaguti because the opecoelid trematodes, while showing similarities with adult allocreadiids, are a well defined group with cotylomicrocercous cercariae. Also, we are not entirely in agreement with the more recent views of Dollfus

(1960) who split the Opecoelidae into several families. The more conservative views of Manter (1947) and of Cable (1956) are followed here.

*Family HAPLOSPLANCHNIDAE*
*Haplosplanchnus (Schikhobalotrema) acutus*
(Linton, 1910) Manter, 1937
(fig. 16)

*Host.*—*Abudefduf saxatilis* (Linn.); sergeant-major; new host record; family Pomacentridae.

*Incidence of infection.*—In 1 of 1 host.

*Location.*—Intestine.

*Locality.*—Galeta Point, Republic of Panama [new locality record].

*Discussion.*—Sogandares (1959) pointed out that *H. acutus* is a parasite of needlefishes (family Belonidae) and reviewed the occurrence of this species in different hosts and localities. The record of *H. acutus* by Manter (1940c) from *Kyphosus elegans* (Peters) in the Galapagos Islands, by Sogandares (1959) from *Thyrinops pachylepis* (Günther) in Panama Bay, and from *Abudefduf saxatilis* in the Panama Atlantic probably represent accidental infections since only one specimen was found in each case.

Our specimen from *A. saxatilis* had no eggs in the uterus, though it agreed in all details with material of the same species from Bimini, Bahamas and Panama Bay.

The Russian workers Skrjabin and Guschanskaja (1955) named the genus *Schikhobalotrema* for *Haplosplanchnus acutus* (Linton, 1910) Manter, 1937, and synonymized *Laruea* Srivastava, 1939 with *Haplosplanchnus* Looss, 1902. Manter (1957) independently arrived at the same conclusions utilizing somewhat different criteria from those of Skrjabin and Guschanskaja (1955). Yamaguti (1958) recognized *Schikhobalotrema*, but regarded *Laruea* a valid genus. Siddiqi and Cable 1960 recognized *Schikhobalotrema* with some reservations even though they named two new species and reported three others in this genus. These authors stated that, while they accepted Skrjabin's and Guschanskaja's arrangement, it would not be surprising to find intermediate species which would invalidate *Schikhobalotrema*. Skrjabin and Guschanskaja (1955) believed that *Schikhobalotrema* could be separated from *Haplosplanchnus* on the basis of the anterior reduction of the vitellaria, presence of a ventral acetabular peduncle, and a poorly developed seminal vesicle in the latter genus. Manter's (1957) views were that *Haplosplanchnus pachysomus* (Eysenhardt, 1829) Looss, 1902 (type species), *H. purii* Srivastava, 1939, and *H. caudatum* (Srivastava, 1939) Skrjabin and Guschanskaja, 1955 (= *Laruea caudata*), all occur in mullets (genus *Mugil* Linn.), possess uterine eggs with occulate miracidia, and have greatly reduced vitellaria. He also suggested that the other species of *Haplosplanchnus*, forms occurring in acanthurid, spariosomid (= family Scaridae), scarid and girellid fishes, with extensive follicular vitellaria, "(which tend to become tubular as happens in the Haploporidae)", and have uterine eggs with undeveloped embryos, should probably be placed in a separate genus. He did not name a new genus for these forms. Manter (1957) was unaware of Skrjabin and Guschanskaja (1955) because at that time political boundaries precluded free exchange of scientific information between Russian and American scientists. The fact remains that the different authors arrived at the same conclusions independently and through the use of different criteria. We have examined many live and preserved specimens of *H. acutus*, (type species of *Schikhobalotrema*), from needlefishes in Bimini, Bahamas. The vitellaria of *H. acutus* are frequently diffuse and poorly developed anteriorly. While there is a tendency for the vitellaria to become tubular in some species of *Haplosplanchnus*, as Manter (1957) suggests, the species of this genus show various degrees of intergradation of this character. We do not believe that the developmental rate of uterine eggs with occulate miracidia should have generic value, at least until we know if fully developed and passed eggs of *H. acutus* also possess occulate miracidia. The fact that the species with occulate miracidia in the uterine eggs coincidentally occur in *Mugil* spp. may indeed be suggestive that these species are closely related, yet not necessarily generically distinct from other species in which the miracidia in the uterine eggs have not developed completely. The only life history study in the Haplosplanchnidae is that of *H. acutus* by Cable (1954) and he was unable to observe (or at least did not report) fully embryonated eggs of this species. The

Figures 15-21. **15.** *Hamacreadium mutabile,* dorsal view of much contracted specimen. **16.** *Haplosplanchnus* (*Schikhobalotrema*) *acutus,* dextrolateral view of whole mount. **17.** *Haplosplanchnus* (*Schikhobaloterma*) *pomacentri,* ventral view of whole mount. **18.** *Multitestis chaetodoni* from *Chaetodon ocellatus,* ventral view. **19.** *Multitestis chaetodoni* from *Chaetodon capistratus,* ventral view. **20.** *Multitestis chaetodoni* from *Chaetodon capistratus,* sketch of cirrus sac showing preprostatic muscular bulb when confused with anterior prostatic vesicle. **21.** *Neoapocreadium coili,* ventral view of a mechanically excysted metacercaria.

length of the acetabular peduncle and poorly developed seminal vesicle are characters which vary in degree only, thus could hardly be considered generic. Another view is that the overlap of certain characters between the species of *Schikhobalotrema* and *Haplosplanchnus* gives further evidence of the closeness of relationship between the two genera. The question remains at present a matter of opinion.

Precluding a knowledge of life histories, when closely allied species groups of adult trematodes show morphological intergradation allowing partial but not complete segregation of these groups (clear-cut characters found in only one species group), we prefer to regard these species groups as subgenera. A moderate approach in naming genera eliminates the need of hastily erecting higher categories (often with insufficient evidence) such as subfamilies which may later tend to confuse the issue. Subgenera have permanent status in nomenclature and show relationships of the species groups without the necessity of creating higher categories.

We presently recognize the following disposition of the species of *Haplosplanchnus:* (1) subgenus *Haplosplanchnus, H. (H.) pachysomus* (Eysenhardt, 1829) Looss, 1902, *H. (H.) purii* Srivastava, 1939; (2) subgenus *Laruea, H. (L.) caudatum* Srivastava, 1939; and (3) subgenus *Schikhobalotrema, H. (S.) acutus* (Linton, 1910) Manter, 1937, *H. (S.) adacutum* Manter, 1937, *H. (S.) brachyurus* Manter, 1937, *H. (S.) girellae* Manter and Van Cleave, 1951, *H. (S.) kyphosi* Manter, 1947, *H. (S.) obtusum* (Linton, 1910) Manter, 1937, *H. (S.) pomacentri* Manter, 1937, and *H. (S.) spariosomae* Manter, 1937.

As Manter (1957) suggested, the haploporids may be related with the haplosplanchnids. Adult specimens of both families sometimes possess sensory papillae on the oral suckers, and except for the presence of a single cecum in *Haplosplanchnus* and a hermaphroditic sac in *Haploporus* Looss, 1902, are similar. We do not know the significance of the similarities between these families. The similarities may represent convergence which is frequently encountered in the Digenea.

*Haplosplanchnus (Schikhobalotrema) pomacentri* Manter, 1937
(fig. 17)

*Host.—Pomacentrus leucostictus* Müller and Troschel, beau gregoire; and *Pomacentrus planifrons* (Cuv. and Val.); *petite jacquette*, new host record; family Pomacentridae.

*Incidence of infection.*—In 1 of 4 *P. leucostictus* and 2 of 2 *P. planifrons.*

*Location.*—Intestine.

*Locality.*—Galeta Point, Republic of Panama [new locality record].

*Discussion.—H. pomacentri* formerly was known only from fishes of the genus *Pomacentrus:* from Tortugas, Florida, in *P. leucostictus* and *P. xanthurus* Poey, (Manter, 1937, Manter, 1947), and from Galapagos Islands, in *P. rectifraenum* Gill, (Manter, 1940c).

One specimen of *H. pomacentri* in our collection lacks a testis.

*Family LEPOCREADIIDAE*
*Subfamily Lepocreadiinae*
*Multitestis chaetodoni* Manter, 1947
(figs. 18-20)

*Hosts.—Chaetodon capistratus* Linn.; four-eyed butterfly fish; and *Chaetodon ocellatus* Bloch; common butterfly fish; family Chaetodontidae.

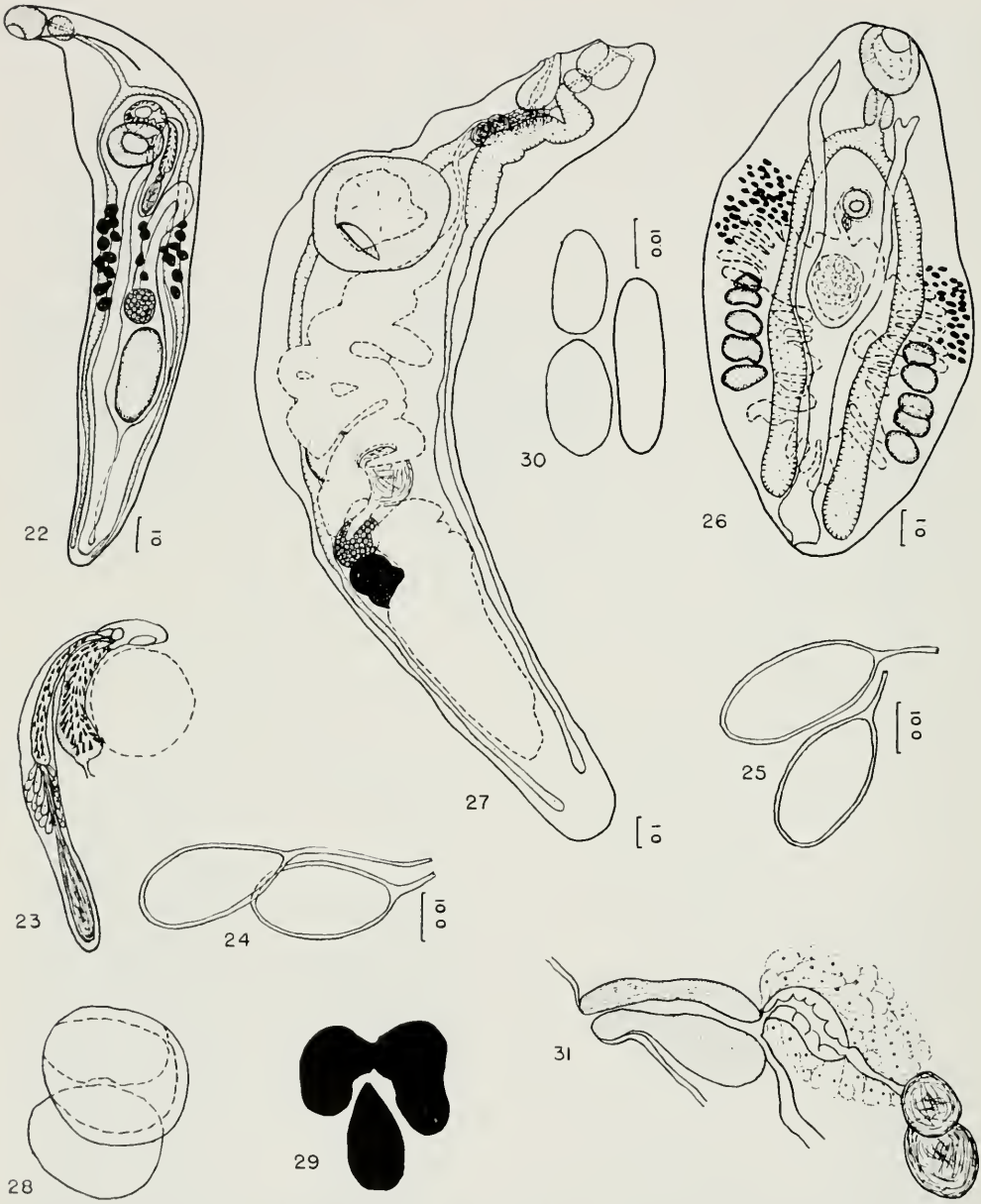
*Incidence of infection.*—In 4 of 5 *C. capistratus* and 2 of 2 *C. ocellatus.*

*Location.*—Intestine.

*Locality.*—Galeta Point, Republic of Panama [new locality record].

*Discussion.*—The only other record of *Multitestis chaetodoni* Manter, 1947, is the original description of specimens from *Chaetodon capistratus* and *C. ocellatus* in Tortugas, Florida. According to Manter (1947), Linton's (1910; p. 115) *Distomum* sp. is *M. chaetodoni.*

Manter (1947) described a bipartite prostatic vesicle for *M. chaetodoni.* Some of our specimens which are darkly stained appear to have a bipartite prostatic vesicle. We obtained a series of 24 specimens of *M. chaetodoni* from *C. ocellatus* and 6 from *C. capistratus,* and have observed that what appears to be the anterior prostatic vesicle in darkly stained specimens is a sphincter muscle at the junction of the prostatic vesicle with the base of the cirrus (fig. 20). If the anterior border of this sphincter muscle




Figures 22-31. **22.** *Hurleytrematoides chaetodoni* from *Chaetodon striatus*, ventral view. **23.** *H. chaetodoni* from *C. striatus*, sketch of dorsal view of terminal genitalia, dashed lines represent outline of acetabulum. **24.** *H.chaetodoni* from *C. striatus*, eggs with polar filaments partially omitted. **25.** *H. chaetodoni* from *C. ocellatus*, eggs with polar filaments partially omitted. **26.** *Siphodera vinaledwardsi*, ventral view of whole mount. **27.** *Theletrum magnasaccum*, sp. nov., ventro-lateral view of holotype, dashed lines represent the position occupied by the uterus. **28.** *T. magnasaccum*, lateral view of vitelline follicles, dashed lines represent optical sections of anterior and posterior follicles. **29.** *T. magnasaccum*, optical reconstruction of vitelline follicles as they would presumably appear in ventral view. **30.** *T. magnasaccum*, uterine eggs. **31.** *T. magnasaccum*, lateral view of terminal genitalia.

is contracted, allowing sperm to collect and swell its internal sperm duct, the muscular bulb could easily be confused with a prostatic vesicle. The cytological details of the wall of the sphincter bulb further suggest that this structure is not a prostatic vesicle. Our specimens had from 9 to 11 testes.

*Subfamily Homalometrinae*
*Neoapocreadium coili* (Sogandares, 1959) Siddiqi and Cable, 1960
(fig. 21)

*Host.*—*Halichoeres bivitattus* (Bloch); slippery dick; family *Labridae.*

*Incidence of infection.*—In 1 of 2 hosts.

*Location.*—Intestine.

*Locality.*—Galeta Point, Republic of Panama [new locality record].

*Discussion.*—The metacercariae of *N. coili* reported here were encysted in muscle fragments of a crustacean (probably a small snapping shrimp) found in the intestine of *H. bivittatus.* The cysts were teased apart with a needle and the metacercariae fixed with A.F.A. between a coverslip and slide. Since we did not have a compound microscope with us, the flame cell pattern and other important details of the live specimens were unobserved.

Sogandares (1959) noted that certain species of *Apocreadium* (*A. bravoi* Sogandares, 1959, *A. coili* Sogandares, 1959, and *A. angustum* Sogandares, 1959) possessed oral suckers with 2 lateral fleshy lobes, and vitellaria confluent anterior to the acetabulum. Siddiqi and Cable (1960) named the genus *Neoapocreadium* for these species. The distinctive oral sucker immediately related our specimens to the genus *Neoapocreadium.* Comparison of our Panama specimens with preadults of *A. coili* and other *Neoapocreadium* spp. collected by one of us (F.S.) in Bimini, Bahamas, leaves little doubt of the specific identity of specimens in the present collection. The type material of *A. coili* is from *Balistes capriscus* Gmelin and *B. vetula* Linn., in Bimini, Bahamas. Siddiqi and Cable (1960) reported *N. coili* from *B. vetula* in Puerto Rico.

*Family MONORCHIIDAE*
*Hurleytrematoides chaetodoni* (Manter, 1942) Yamaguti, 1953
(figs. 22-25)

*Hosts.*—*Chaetodon capistratus* Linn.; four-eyed butterfly fish; *Chaetodon ocellatus* Bloch; common butterfly fish; and *Chaetodon striatus* Linn., banded butterfly fish; new host record; family *Chaetodontidae.*

*Incidence of infection.*—In 2 of 5 *C. capistratus;* 1 of 2 *C. ocellatus;* and 1 of 1 *C. striatus.*

*Location.*—Intestine.

*Locality.*—Galeta Point, Republic of Panama [new locality record].

*Discussion.*—Manter (1942, 1947) described and reported *Hurleytrema chaetodoni* from *Chaetodon ocellatus* and *C. capistratus* in Tortugas, Florida. The metraterm of his type specimens was about 3/4 length of the cirrus sac. The metraterm in our material shows considerable extension or contraction (figs. 22, 23), sometimes agreeing in proportion with the type description. The egg sizes of *H. chaetodoni* from *Chaetodon striatus* and *C. ocellatus* (figs. 24, 25) overlap, though they are considerably shorter (about 30 to 32 *vs.* 40 to 46 microns) than those reported by Manter (1942). The unipolar filament-egg ratio of our specimens agrees with Manter's (1942) description. Although we have no material of *H. chaetodoni* from localities intermediate between Tortugas and Panama, these variations in egg size may represent population differences. Siddiqi and Cable (1960) reported *H. chaetodoni* from *Chaetodon capistratus* in Puerto Rico.

Yamaguti (1953) erected a new genus *Hurleytrematoides* for *H. chaetodoni.* The description of the type species of *Hurleytrema, H. ovocaudatum* Srivastava, 1938, seems to differ from that of *H. chaetodoni* mainly in the type of cirrus and metraterm spines, in egg size, and in a more posterior distribution of the vitelline follicles. Professor H. W. Manter (personal communication) adds another distinguishing character and recognizes *Hurleytrematoides* on the basis of a bipartite seminal vesicle. We are following his views here in recognizing *Hurleytrematoides.*

*Family CRYPTOGONIMIDAE*
*Subfamily Siphoderinae*
*Siphodera vinaledwardsi* (Linton, 1901) Linton, 1910
(fig. 26)

*Host.*—*Lutjanus synagris* (Linn.); lane snapper; and *Ocyurus chrysurus* (Bloch); yellow-tail; family Lutjanidae.

*Incidence of infection.*—In 2 of 2 *L. synagris* and 2 of 2 *O. chrysurus.*

*Location.*—Intestine.

*Locality.*—*L. synagris* from Cristobal Yacht Club basin and Galeta Point and *O. chrysurus* from Galeta Point, Republic of Panama [new locality record].

*Discussion.*—The distribution of *S. vinaledwardsi* was recently reviewed by Sogandares and Hutton (1959). These authors neglected to cite the following records: Bravo (1956) in *Lutjanus guttatus* (Steindachner) from Baja California, Mexico; Sparks (1957) in *Ocyurus chrysurus* from Nassau, Bahamas; and Sogandares (1959) in *Lutjanus synagris* from Bimini, Bahamas. Siddiqi and Cable (1960) reported *S. vinaledwardsi* from *Lutjanus synagris* and *L. analis* from Puerto Rico.

*S. vinaledwardsi* is a widespread species in the American Atlantic and utilizes various carnivorous definitive hosts, mainly lutjanid, batrachoidid, and pomadasyid fishes.

Our specimens from the Atlantic coast of Panama compare favorably with those collected in other localities in Florida and Bimini, Bahamas.

*Family HEMIURIDAE*
*Subfamily Lecithasterinae*
*Theletrum* **magnasaccum,** sp. nov.
(figs. 27-31)

*Host.*—*Abudefduf saxatilis* (Linn.); sergeant-major; family pomacentridae.

*Incidence of infection.*—In 1 of 1 host.

*Location.*—Stomach.

*Locality.*—Galeta Point, Republic of Panama.

*Holotype.*—U. S. Nat. Mus. Helm. Coll. No. 39500.

*Diagnosis* (based on one specimen).—*Theletrum:* Body elongate, approximately 3.15 long by 0.59 wide at midbody. Cuticle smooth, bearing no papillae. Forebody 0.66 long. Oral sucker subterminal, 0.16 long by 0.17 wide. Preoral lip present. Acetabulum 0.44 long by 0.42 wide. Sucker ratio about 1:2.4. Prepharynx so short that it appears absent. Pharynx roundish, 0.07 long by 0.10 wide. Esophagus very short, almost appearing absent. Ceca extending, one on each side of body, to posterior end of body. Genital pore ventral, median, at level of midpharynx. Sinus sac connecting directly with genital pore, muscular, pear-shaped; 0.10 long by 0.10 at widest portion. Testes equatorial, oblique; sinistral testis anteriormost, 1/7 distance from acetabulum to posterior end of body, oval in shape, about 0.14 long by 0.19 wide; dextral testis posteriormost, about 1/3 distance from acetabulum to posterior end of body, roundish in shape, about 0.15 long by 0.17 wide. Seminal vesicle intercecal, about 1/3 distance from acetabulum to anterior end of body, bipartite; connecting with a short prostatic vesicle which is surrounded by prostate cells and is about 1/2 length of the sinus sac with which it connects (fig. 31). Ovary slightly less than 1/2 distance from acetabulum to posterior end of body, oblong in shape, about 0.12 long by 0.13 wide. Seminal receptacle conspicuous between posterior testis and dorsal aspect of ovary, spherical and larger than ovary. Vitellaria of two compact lobes (figs. 28, 29), anterior vitellarium bilobed, posterior vitellarium unlobed; immediately posterior to and in contact with ovary. Uterus with large sac-like coils which are difficult to trace, mainly intercecal, descending from ovarian complex to fill most of postovarian area, ascending to cover partially the vitellaria, seminal receptacle, ovary, and testes, intruding between ovary and posterior testis and foretestis, the sac-like coils disappearing anterior to acetabulum where uterus perforates the sinus sac adjacent to the connection with prostatic vesicle. Eggs thick-shelled, varible in shape and size (fig. 29), about 17.4 to 31.9 microns long by 11.6 to 14.0 microns wide. Excretory vesicle not observed.

*Discussion.*—The genus *Theletrum* Linton, 1910 resembles *Aponurus* Looss, 1907, differing mainly by possessing 2 or 3 instead of 7 or 8 prominent vitelline lobes. Studies of additional species may show that these two genera are synonymous or that *Theletrum* is a subgenus at best. At present the vitelline lobation appears to be a stable, though sometimes difficult to observe, character. Yamaguti (1958) reexamined Linton's type material of *T. fustiforme* and believed that, "the ejaculatory duct and metraterm open into a genital atrium." Yamaguti also stated, ". . . the cirrus pouch could not be made out with certainty." Manter (1947) studied specimens of *T. fustiforme* from the type host and locality and did not report or picture a genital atrium. Instead he stated,

TABLE 1.
*Nine digenetic trematodes from the Atlantic coast of Panama and their distribution in the American Pacific and Atlantic* [2]

| Species | Localities | | |
|---|---|---|---|
| | Tropical American Pacific | Tropical American Atlantic other than Panama | American Atlantic from Woods Hole, Mass. to Beaufort, N. C. |
| *Bucephaloides arcuatus* | — | + | + |
| *Hamacreadium mutabile* | + | + | — |
| *Haplosplanchnus acutus* | + | + | — |
| *Haplosplanchnus pomacentri* | + | + | — |
| *Multitestis chaetodoni* | — | + | — |
| *Neoapocreadium coili* | — | + | — |
| *Hurleytrema chaetodoni* | — | + | — |
| *Siphodera vinaledwardsi* | + | + | + |
| *Theletrum magnasaccum* | — | — | — |

[2] (+) denotes presence and (—) absence of the species.

"The seminal vesicle is a long coiled tube, slightly overlapping the acetabulum; the pars prostatica is rather short, its distal half surrounded by a compact but conspicuous prostatic gland. The sinus sac is cylindrical, almost straight, with thick walls, containing a few gland cells." Our study of the terminal genitalia of *T. magnasaccum* lends allied support to Manter's (1947) observations and redescription of the terminal genitalia of *T. fustiforme*. The "prostate gland" described by Manter is doubtless a prostatic vesicle surrounded by prostate cells. There are three species in *Theletrum*, *T. fustiforme* Linton, 1910 (type species), *T. lissosomum* Manter, 1940 and *T. gravidum* Manter, 1940. *T. magnasaccum* resembles *T. gravidum* and *T. lissosomum* but differs by possessing a conspicuous hermaphroditic sac, two vitelline lobes, a bipartite seminal vesicle, and other small differences which are at present difficult to evaluate due to the present shortage of material. *T. magnasaccum* differs from *T. fustiforme* by lacking the postacetabular ventral folds and papillae as described by Manter (1947), in genital pore position and by possessing a bipartite seminal vesicle which does not overlap the acetabulum.

*T. magnasaccum* is closely related with *T. gravidum*, from the same host genus (*Adudefduf*) in the Pacific, and probably represents its geminate species in the Atlantic.

The vitelline lobes of *T. magnasaccum* initially resembled those of *Aponurus* when viewed laterally. Careful focussing with the microscope showed that the mass is composed of two follicles (fig. 28), the anteriormost is apparently bilobed. Figure 29 shows an optical reconstruction as the vitelline lobes would presumably appear in frontal view.

One striking feature about *T. magnasaccum* is the size and shape of the eggs. Figure 30 shows three different types of eggs, from the same portion of the uterus, which we observed. Care was taken to assure that

TABLE 2.
*Host species examined and trematodes found.*

*Abudefduf saxatilis* (Linn.)
  *Haplosplanchnus acutus* (Linton, 1910) Manter, 1937
  *Theletrum magnasaccum* (this paper)
*Acanthurus chirurgus* (Bloch)
  no trematodes found
*Chaetodon capistratus* Linn.
  *Hurleytrematoides chaetodoni* (Manter, 1942) Yamaguti, 1953
  *Multitestis chaetodoni* Manter, 1947
*Chaetodon ocellatus* Bloch
  *Hurleytrematoides chaetodoni* (Manter, 1942) Yamaguti, 1953
  *Multitestis chaetodoni* Manter, 1947
*Chaetodon striatus* Linn.
  *Hurleytrematoides chaetodoni* (Manter, 1942) Yamaguti, 1953
*Eucinostomus californiensis* (Gill)
  no trematodes found
*Gymnothorax funebris* Ranzani
  no trematodes found
*Halichoeres bivittatus* (Bloch)
  *Neoapocreadium coili* (Sogandares, 1959) Siddiqi and Cable, 1960
*Lutjanus griseus* (Linn.)
  one trematode found but lost by maceration, probably a *Mctadena* sp.
*Lutjanus synagris* (Linn.)
  *Siphodera vinaledwardsi* (Linton, 1901) Linton, 1910
*Ocyurus chrysurus* (Bloch)
  *Hamacreadium mutabile* Linton, 1910
*Pomacentrus leucostictus* Müller and Troschel
  *Haplosplanchnus pomacentri* Manter, 1937
*Pomacentrus planifrons* (Cuvier and Valenciennes)
  *Haplosplanchnus pomacentri* Manter, 1937
*Sphyraena barracuda* (Walbaum)
  *Bucephaloides arcuatus* (Linton, 1900) Hopkins, 1954
*Thalassoma bifasciatum* (Bloch)
  no trematodes found

these eggs were not tilted, creating an illusion of shortness. The majority of the uterine eggs were of the narrow, elongate, sausage-shaped type.

The name *magnasaccum* is for the large sinus sac (*magna* = large) (*saccum* = sac).

Manter's and Pritchard's (1960) views regarding the higher categories of the Hemiuridae have been followed in placing *Theletrum* in the Lecithasterinae.

## The Geographic Distribution of Digenea Reported in this Paper

Table 1 shows the American distribution of the Digenea reported here. Six species are known only from the Atlantic Ocean, while four are shared with the Pacific. Eight species are found in other tropical American Atlantic localities, two of these species as far north as Woods Hole, Massachusetts.

The present sample is too small to determine significant faunal differences. We believe that the digenetic trematode fauna from the Atlantic coast of Panama will reveal a closer resemblance to that of Tortugas, Florida, and the Bahamas Islands than to that from the Pacific coast of Panama. The fish and molluscan fauna of Tortugas, Florida, and the Bahamas Islands is more like that of the Atlantic than the Pacific side of Panama. Even though our sample was small, every fish host, except *Pomacentrus planifrons* occurs in Tortugas, Florida, and the Bahamas Islands. Table 2 lists the host species examined and trematodes found.

## Summary

Nine digenetic trematodes, including the description of a new species, *Theletrum magnasaccum*, (Hemiuridae: Lecithasterinae), are reported from fifteen species of marine fishes of the Atlantic coast of Panama. The systematic status, distribution, hosts, and new information on the morphology of each trematode species is discussed.

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## ABSTRACT

Nine digenetic trematodes of marine fishes from the Atlantic coast of Panama are reported: *Bucephaloides arcuatus* (Linton, 1900) (*Bucephalidae*), from the pyloric ceca of *Sphyraena barracuda* (Walbaum) (*Sphyraenidae*); *Hamacreadium mutabile* Linton, 1910 (Opecoelidae), from the intestine of *Ocyurus chrysurus* (Bloch) (Lutjanidae); *Haplosplanchnus* (*Schikhobalotrema*) *acutus* (Linton, 1910) (Haplosplanchnidae), from the intestine of *Abudefduf saxatilis* (Linn.) (Pomacentridae); *Haplosplanchnus* (*Schikhobalotrema*) *pomacentri* Manter, 1937 (Haplosplanchnidae), from the intestines of *Pomacentrus leucostictus* Müller and Troschel, and *P. planifrons* (Cuv. and Val.) (Pomacentridae); *Multitestis chaetodoni* Manter, 1947 (Lepocreadiidae), from the intestines of *Chaetodon capistratus* Linn. and *C. ocellatus* Bloch (Chaetodontidae); the metacercaria of *Neoapocreadium coili* (Sogandares, 1959) (Lepocreadiidae), encysted in crustacean muscle remains from the intestine of *Halichoeres bivitattus* (Bloch) (Labridae); *Hurleytrematoides chaetodoni* (Manter, 1942) (Monorchiidae), from the intestines of *Chaetodon capistratus* Linn., *C. ocellatus* Bloch, and *C. striatus* Linn. (Chaetodontidae); *Siphodera vinaledwardsi* (Linton, 1901) (*Cryptogonimidae*), from the intestines of *Lutjanus synagris* (Linn.) and *Ocyurus chrysurus* (Bloch) (Lutjanidae); and *Theletrum magnasuccum* (this paper) (Hemiuridae), from the stomach of *Abudefduf saxatilis* (Linn.) (Pomacentridae). The systematic status, distribution, hosts and new information on the morphology of each trematode species is discussed.

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# TULANE STUDIES IN ZOOLOGY

Volume 8, Number 6 July 14, 1961

## THE FEMALE REPRODUCTIVE CYCLE OF THE CRAYFISH *CAMBARELLUS SHUFELDTI:* THE INFLUENCE OF ENVIRONMENTAL FACTORS

MILDRED EILEEN LOWE,
*DEPARTMENT OF ZOOLOGY, UNIVERSITY OF MELBOURNE, MELBOURNE, AUSTRALIA*

## FECUNDITY AND REPRODUCTION IN THE LARGESCALE MENHADEN, *BREVOORTIA PATRONUS* GOODE

ROYAL D. SUTTKUS
and
BANGALORE I. SUNDARARAJ,
*DEPARTMENT OF ZOOLOGY, TULANE UNIVERSITY, NEW ORLEANS, LOUISIANA*

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# THE FEMALE REPRODUCTIVE CYCLE OF THE CRAYFISH *CAMBARELLUS SHUFELDTI:* THE INFLUENCE OF ENVIRONMENTAL FACTORS[1]

MILDRED EILEEN LOWE,

*Department of Zoology, University of Melbourne, Melbourne, Australia*

Many organisms show a reproductive periodicity correlated with environmental factors. Photoperiodism and response to changing temperature are the best known phenomena. Food and rainfall and, in marine organisms, changes in salinity and changes in pressure due to spring tides, may also affect time of egg-laying.

Most of the research on influence of photoperiodism upon reproductive cycles in invertebrates concerns induction of diapause in insects. This subject was reviewed by Lees (1955). Most insects may be classified as "long-day" species; that is, exposure to long day-lengths allows uninterrupted development while short day-lengths favor diapause. However, in many insects extremely short day-lengths or constant darkness may also prevent diapause.

High temperatures augment the effect of long day-lengths in preventing diapause, while low temperatures favor its onset. For the termination of diapause, temperature may be more important than day-length as many insects require a period of chilling before diapause terminates (Lees, 1955).

By increasing the temperature in midwinter Loosanoff and Davis (1952) initiated a second breeding season in the oyster *Crassostrea virginica* which normally breeds only during the summer. Low temperature stimulated breeding in *Balanus*, while spawning occurred both at time of maximum and of minimum temperatures in the limpet *Patella vulgata* (Giese, 1959).

Korringa (1952) showed that temperature is not the only factor influencing spawning. Within the spawning season of the European oyster, *Ostrea edulis*, semimonthly peaks of reproductive activity are correlated with spring tides. In this and other animals exhibiting increased activity two times each lunar cycle, the increased water pressure of spring tides might be the triggering influence. Monthly spawning, as in the palolo worm, is believed to be iniated by increased photoperiod (reviewed by Korringa, 1947).

Among the Crustacea, G. J. Stephens (1952) showed, in *Orconectes virilis*, that increased day-length accelerated the rate of the normal cyclic increase and decrease in ovarian size. She also demonstrated that constant darkness completely interrupted cyclic activity, the oocytes developing to a mature condition and remaining in that state. However, Suko (1958) showed that the response of *Procambarus clarkii* to darkness depends on the state of the ovary when the animal is placed in the darkness. With another crayfish, *Orconectes rusticus*, G. C. Stephens (1952) showed that light caused modifications of a secondary sexual structure, the cement glands, which secrete a substance used in attaching the newly-laid eggs to the pleopods. These glands were stimulated to develop at a more rapid rate in animals under increased photoperiods.

The present investigation was undertaken to define the female reproductive cycle of the crayfish *Cambarellus shufeldti*. This small crayfish is readily available in southeastern Louisiana throughout the year. It has been used in studies on chromatophores, retinal pigment migration, metabolism, and on the endocrine factors controlling these functions (*e.g.*, Fingerman, 1957; Fingerman and Lowe, 1957). The only studies of the life cycle of this species were the brief ecological surveys of Penn (1942, 1950) who reported an almost continual period of reproduction with peak activity in late winter, continuing high through early summer.

The series of observations presented here represents an attempt (1) to outline in detail the female reproductive cycle of this crayfish, and (2) to obtain information concerning environmental factors that may regulate the cycle.

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[1] Most of this paper is a portion of a dissertation submitted in partial fulfilment of the requirements for the Ph.D. degree in zoology at Tulane University, New Orleans, Louisiana, 1959.

## Materials and Methods

Adult specimens of *Cambarellus shufeldti* are small, the female averaging only 20 mm in length. Typically they inhabit shallow fresh-water ponds and ditches that are exposed to direct sunlight part of each day and that contain an abundant plant growth (Penn, 1942, 1950). The population studied occurred in a roadside ditch, in pinelands, near Pearl River, Louisiana. The principal water plants present were *Scirpus nanus* and *Rhyncospora* spp. Other crayfishes associated with *Cambarellus* were *Orconectes clypeatus* and *Procambarus blandingi acutus.*

The water level in the ditch fluctuated from approximately 18 inches to below ground level according to the amount of rainfall. Very little rain fell during late autumn of 1958 and the ditch was dry from the middle of December to the third week in January, 1959. The crayfish can survive such droughts by burrowing. They evidently do not burrow unless there is no standing water as a small December collection was obtained from only one-half inch of water by raking through plant growth. At all other periods during the study the crayfish were active and were obtained with dipnets. Although a thin film of ice formed over the water surface in February, 1958, animals were still present in the water.

Animals were collected at least once a month from November, 1957, through November, 1959, preserved in Bouin's fixative, and stored in 70 percent ethyl alcohol. The weights and measurements presented below are those obtained from preserved crayfish. The animals were blotted and weighed to the nearest milligram. Cephalothorax length, from tip of rostrum to posterior margin of carapace, was measured to the nearest 0.5 mm with the aid of dividers and a stereoscopic microscope.

The degree of cement gland development and the presence or absence of a plug in the oviducts were noted. In *C. shufeldti* the cement glands underlie the anterior portions of the second through sixth abdominal segments at the junction of the sterna and pleura and the mid-ventral line along the strong transverse bar present in each sternum. The glands extend into the protopodite and endopodite of each pleopod and into both the exopodite and endopodite of the uropods. The degree of cement gland development was determined according to the stages of G. C. Stephens (1952): stage 1. Numerous tiny, milky-white translucent, circular or subcircular spots appear in areas of future gland development; stage 2. The white areas enlarge and subcircular transparent areas appear within them; stage 3. The glands appear as translucent white lobate clusters surrounding the original white areas in an irregular manner; stage 4. The glands become opaque, milky-white and so filled with secretion that their lobate character is difficult to distinguish.

In *Cambarellus* the mid-ventral glands mature slowly and may still be in stage 2 or 3 when the lateral glands are in the fully developed stage 4. Therefore, the states of the two sets of glands were recorded separately. A stage listed as 4.0, 2.0 would indicate that the lateral glands were at stage 4, the mid-ventral only at stage 2.

After the specimens had been examined grossly their ovaries were removed. The ovary is Y-shaped with two anterior and one posterior lobes located immediately ventral to the heart; the anterior lobes curve dorsally around its anterior end. The oviducts originate from the ventro-lateral surface of the ovary where the three lobes join. Camera lucida drawings were made of the ovaries before removal from the animal, with the crayfish held in a lateral and slightly dorsal position.

The diameters of the largest oocytes in each ovary were measured to the nearest 0.01 mm with an ocular micrometer and the average diameter of the four largest was recorded. Each ovary was weighed to the nearest 0.1 mg. after being touched to a piece of filter paper and placed in a dry, covered weighing bottle. The weight of any moisture remaining in the weighing bottle when the ovary was removed was subtracted from the previously recorded weight.

## Results and Discussion

### *The Normal Yearly Reproductive Cycle*

Animals were collected at least once a month from November, 1957, through November, 1959, to determine the normal reproductive cycle. Only animals of 8.5 mm cephalothorax length and larger were considered because only two mature animals smaller than this were found.

A population of *C. shufeldti* has an almost continuous period of reproductive activity. Females bearing eggs or young can be collected nearly every month of the year. The eggs are attached to the female's pleopods, where young hatch from the eggs and remain attached through the second instar. The total time of attachment to the pleopods in *Cambarellus* is about three weeks.

The percentage of females bearing eggs and young is shown in Figure 1. Two peaks of reproductive activity occur, the higher in late winter and a second in early summer. A small rise also occurs in October.

*The life cycle.*—Approximately fifty females from each of the monthly collections from January, 1958, through November, 1959, were weighed and cephalothorax measured. Animals carrying eggs or young were weighed with brood attached. Each month some animals were dissected to determine ovarian condition.

Comparison of total body weight (Tables 1 and 2) shows three distinct groups of females which appear and mature at different times during the year. There is a definite separation between the heaviest animals in one group and the lightest in a second, heavier group present in the population at the same time. Comparison of increment in cephalothorax length produces only a hazy pattern of growth as seen in Table 2 which summarizes the correspondence between weight and length throughout the study.

In January 1958 only one size group of adult females was present. The same group (hereafter referred to as group A) was present in February, showing a small increment in weight and no increase in length. Eighty-five percent of these animals carried eggs or young. The largest juveniles measured 7.5 mm cephalothorax length; they were not weighed.

By March many group A animals had lost their young and molted, and the group showed a large weight increase. A second group of females (group B) had molted to mature size. These latter comprised 36 percent of the adult female population and all were ovigerous. The largest juvenile measured 7.5 mm cephalothorax length.

By April 1958 all remaining group B animals had undergone a maturation molt as the largest juveniles measured only 6.0 mm cephalothorax length. Approximately 50 percent of the group carried eggs or young. All of group A had completed a post breeding molt. These two groups could not be separated on the basis of length as group A measured 9.0-10.5 mm cephalothorax length and group B, 10.0-11.5 mm.

TABLE 1.
*Body weight increment in the three groups throughout the study.*

| Month | Group A | Group B | Group C |
|---|---|---|---|
| 1-58 | 164-206 (190)* | | |
| 2-58 | 190-223 (203) | | |
| 3-58 | 256-310 (284) | 181-200 (190) | |
| 4-58 | 292-387 (340) | 186-215 (192) | |
| 5-58 | 315 | 193-240 (215) | |
| 6-58 | | 268-340 (299) | 196-227 (212) |
| 7-58 | | 329-359 (341) | 148-265 (197) |
| 8-58 | | | 163-253 (199) |
| 9-58 | | | 196-245 (221) |
| 10-58 | | | 235-384 (274) |
| 11-58 | 158-185 (172) | | 292-364 (311) |
| 12-58 | 178-210 (196) | | 300-345 (327) |
| 1-59 | 192-230 (210) | | 377-418 (393) |
| 2-59 | 215-292 (251) | | |
| 3-59 | 256-310 (284) | 167-201 (185) | |
| 4-59 | 305-378 (337) | 179-220 (200) | |
| 5-59 | | 181-250 (220) | |
| 6-59 | | 234-290 (278) | 150-162 (156) |
| 7-59 | | 287-335 (310) | 174-218 (194) |
| 8-59 | | 320-335 (330) | 193-227 (211) |
| 9-59 | | | 208-231 (218) |
| 10-59 | | | 245-286 (265) |
| 11-59 | 160-188 (175) | | 279-317 (299) |

* 164-206 = weight range; (190) = mean.

TABLE 2.
*Monthly weights and cephalothorax lengths of a representative sample of the adult female population.*

| Month | Group | No. Measured & Weighed | Cephalothorax Length (mm) range | mean | Weight (mg) range | mean | % in size class |
|---|---|---|---|---|---|---|---|
| Jan. 1958 | A | 35 | 9.0-10.0 | 9.6 | 164-206 | 190 | 100 |
| Feb. 1958 | A | 41 | 9.0-10.5 | 9.8 | 190-223 | 203 | 100 |
| March 1958 | A | 36 | 9.5-11.0 | 10.0 | 256-310 | 284 | 64 |
| | B | 20 | 9.0- 9.5 | 9.2 | 181-200 | 190 | 36 |
| April 1958 | A | 19 | 10.0-11.5 | 10.5 | 292-387 | 340 | 40 |
| | B | 28 | 9.0-10.5 | 9.7 | 186-215 | 192 | 60 |
| May 1958 | A | 1 | 10.5 | | 315 | | 2 |
| | B | 42 | 9.0-10.5 | 9.8 | 193-240 | 215 | 98 |
| June 1958 | B | 46 | 9.0-11.5 | 10.1 | 268-340 | 299 | 76 |
| | C | 15 | 9.0-10.0* | 9.4 | 196-227 | 212 | 24 |
| July 1958 | B | 6 | 10.5-11.5 | 11.0 | 329-359 | 341 | 12 |
| | C | 44 | 8.5-10.0 | 9.2 | 148-265 | 197 | 88 |
| Aug. 1958 | C | 50 | 8.5-10.0 | 9.2 | 163-253 | 199 | 100 |
| Sept. 1958 | C | 51 | 9.0-10.5 | 9.6 | 196-245 | 221 | 100 |
| Oct. 1958 | C | 50 | 9.5-11.5 | 10.0 | 235-384 | 274 | 100 |
| Nov. 1958 | C | 52 | 9.5-11.5 | 10.2 | 292-364 | 311 | 80 |
| | A | 13 | 9.0- 9.5* | 9.2 | 158-185 | 172 | 20 |
| Dec. 1958 | C | 9 | 10.0-11.5 | 10.6 | 300-345 | 327 | 30 |
| | A | 21 | 9.0-10.0 | 9.6 | 178-210 | 196 | 70 |
| Jan. 1959 | C | 4 | 10.0-11.5 | 11.0 | 377-418 | 393 | 9 |
| | A | 45 | 9.5-10.5 | 10.0 | 192-230 | 210 | 91 |
| Feb. 1959 | A | 45 | 9.5-10.0 | 9.9 | 215-292 | 251 | 100 |
| March 1959 | A | 39 | 9.5-11.0 | 10.1 | 265-315 | 288 | 78 |
| | B | 11 | 9.0- 9.5 | 9.2 | 167-201 | 185 | 22 |
| April 1959 | A | 24 | 10.0-11.5 | 10.6 | 305-378 | 337 | 44 |
| | B | 31 | 9.0-10.0 | 9.6 | 179-220 | 200 | 56 |
| May 1959 | B | 35 | *9.0-10.5 | 9.7 | 181-250 | 220 | 100 |
| June 1959 | B | 48 | 9.5-11.0 | 10.1 | 234-290 | 278 | 92 |
| | C | 4 | *9.0-10.0 | 9.3 | 150-162 | 156 | 8 |
| July 1959 | B | 14 | 10.5-11.5 | 10.8 | 287-335 | 310 | 28 |
| | C | 36 | 8.5-10.0 | 9.2 | 174-218 | 194 | 72 |
| Aug. 1959 | B | 3 | 10.5-11.5 | 11.0 | 320-335 | 330 | 6 |
| | C | 47 | 8.0-10.5 | 9.5 | 193-227 | 211 | 94 |
| Sept. 1959 | C | 35 | 8.5-11.0 | 9.9 | 208-231 | 218 | 100 |
| Oct. 1959 | C | 35 | 9.5-10.5 | 10.2 | 245-286 | 265 | 100 |
| Nov. 1959 | C | 48 | 10.0-11.5 | 10.6 | 279-327 | 299 | 85 |
| | A | 9 | 8.5- 9.5 | 9.0 | 160-188 | 175 | 15 |

* In these groups 8.5 mm animals were present but are not included in the tabulation as their ovaries were in an immature condition.

However, animals measuring 10.0 and 10.5 mm in group A were approximately 100 mg heavier than those of the same length in group B.

Group A comprised only 2 percent of the population by May, 1958. Most group B individuals had lost the young from the pleopods but had not undergone a post-breeding molt.

By June most of group B had molted and 65 percent of these had produced a second brood. A third group of females, group C, had begun to mature and formed 2 percent of the adult female population. Approximately 85 percent of this new group were ovigerous. The ovaries of 8.5 mm females that now appeared in the population were immature.

In July the remainder of group B molted and all the animals were large, 10.5 to 11.5 mm cephalothorax length. This group comprised 12 percent of the population and none was ovigerous. More group C animals had undergone a maturation molt and the

ovaries of 8.5 mm animals reached a mature condition. Group C could be subdivided into two sections, the larger representing those animals hatched at the beginning of the winter breeding season and reproducing in June, the smaller those hatched towards the end of the season and reproducing in July and August.

By August 1958 group B had disappeared from the population. The 18 percent of group C that carried eggs or young was composed of smaller animals, 8.5 to 9.0 mm. There were many juveniles whose cephalothorax length was 8.0 mm. The larger animals had shown no increase in weight.

In September 1958 a number of the animals molted as shown by increase in length, but the weight of the larger animals remained stationary.

By October all the animals molted and there was a large weight increment. The largest animals produced a second brood.

In November the larger animals of group C were dying off without molting again. The group made up 86 percent of the adult females as Group A began to appear in the adult population. The 8.5 mm animals possessed immature ovaries. Only in July and August were such small animals found in a reproductive phase.

In December only a small collection could be obtained due to drought conditions. Group C constituted 30 percent of the adult female population. Some Group A animals had molted but the increment in weight was small.

In late January, 1959, group C was composed of very large, heavy animals, all of which were ovigerous. Group A animals molted but had not yet laid eggs.

By February the entire adult female population was again composed of only one size group, group A, 63 percent of which were carrying eggs or young.

Figure 1 and Tables 1 and 2 show the repetition of this cycle through the rest of 1959.

*Maturation of oocytes.*—In the ovaries of immature animals the oocytes are tiny, 0.40 mm or less in diameter. They are transparent and widely separated by interstitial material. As the animals mature the oocytes begin to grow, become translucent white and then

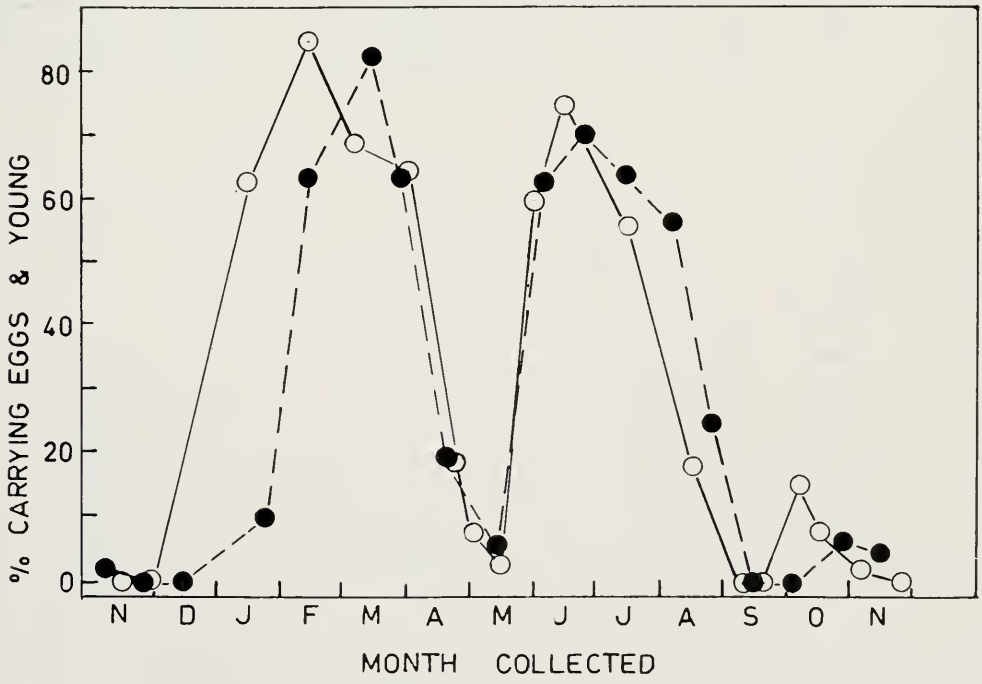


Figure 1. The yearly reproductive cycle of *C. shufeldti* expressed in terms of the percentage of females that were carrying eggs or young. Solid line, circles = Nov. 1957-Nov. 1958; dotted line, dots = Nov. 1958 - Nov. 1959.

opaque ivory at approximately 0.70 mm in diameter. The oocytes later acquire a greenish tinge as yolk deposition increases their size to 1.1 mm. The color of the oocytes gradually deepens to the dark dull green-black of mature eggs, with a diameter of 1.4 to 2.0 mm. Eggs are black immediately after laying. The smallest eggs found attached to the pleopods measured 1.45 mm. The same sequence of oocyte development is repeated after egg-laying occurs.

At times yolk resorption occurs and the oocytes may become a bright chicken-yolk yellow or even orange. Oocytes undergoing resorption become coarsely granular, irregular vacuoles appear within them, and they become surrounded by a clear yellow fluid. When resorption is occurring rapidly the entire ovary may become distended with a pale yellow fluid. As resorption proceeds the oocytes become smaller and their outlines irregular. They eventually disinte-

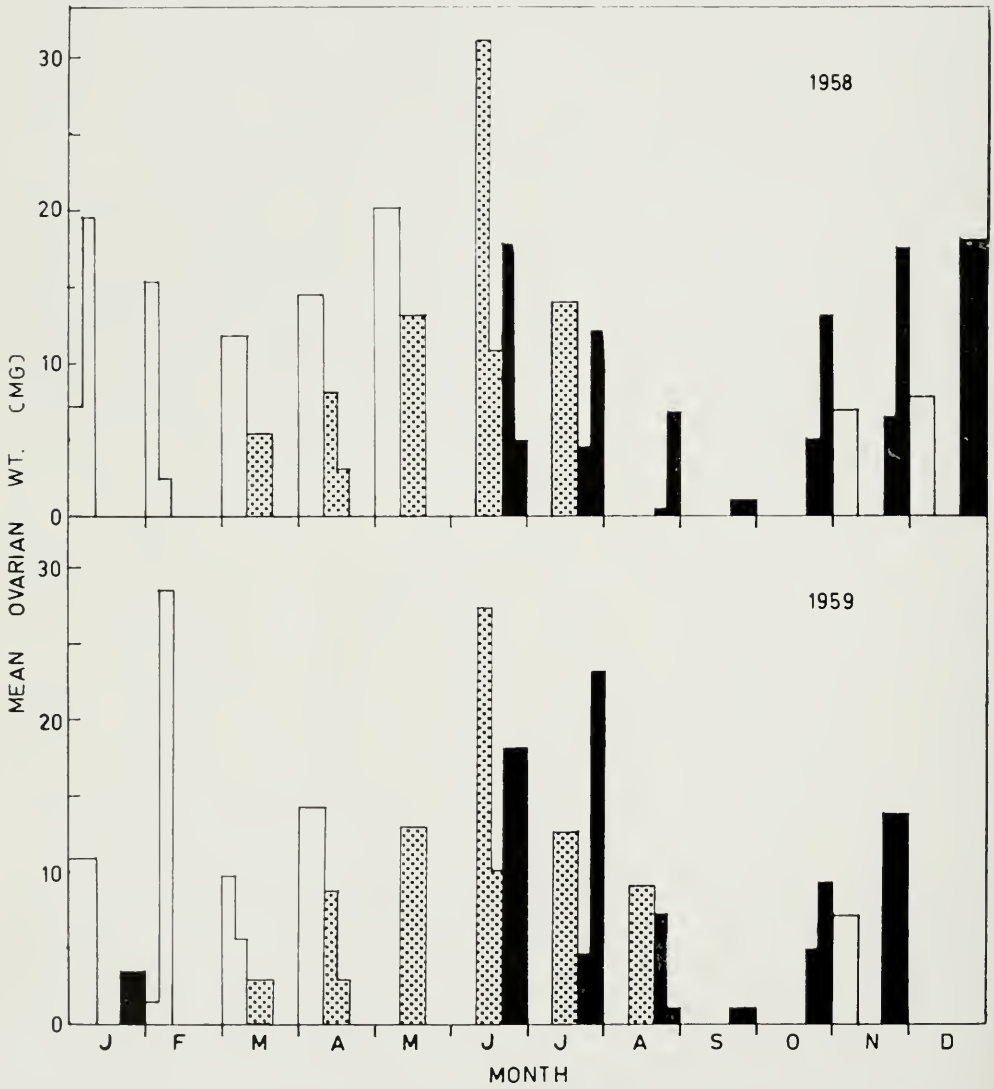


Figure 2. Variation in mean ovarian weight throughout the year. Group A, open; Group B stippled; Group C solid bars. When two values are given for the same group in one month, the lesser value refers to animals carrying eggs or young at time of measurement.

grate leaving loose irregular masses of yellow-orange granules that gradually disappear.

*Ovarian cycle.* — The condition of the ovaries reflects the presence of the three size groups. Thus the ovarian weights of the

TABLE 3.
*Summary of monthly measurements on ovarian weight and oocyte diameter.*

| Month | Group | No. used | Weight of Ovary (mg) range | Weight of Ovary (mg) mean | Oocyte Diameter (mm) range | Oocyte Diameter (mm) mean |
|---|---|---|---|---|---|---|
| 1-58 | A* | 14 | 5.5- 8.2 | 7.2 | 1.17-1.33 | 1.25 |
| | A | 12 | 18.7-20.3 | 19.5 | 1.63-2.00 | 1.83 |
| 2-58 | A- | 13 | 13.2-17.3 | 15.3 | 1.33-1.57 | 1.51 |
| | A* | 10 | 1.7- 2.7 | 2.4 | 0.37-0.67 | 0.49 |
| 3-58 | A*- | 12 | 10.9-19.7 | 11.8 | 0.92-1.16 | 0.98 |
| | B* | 15 | 5.2- 5.6 | 5.4 | 0.58-0.68 | 0.64 |
| 4-58 | A- | 14 | 13.9-15.6 | 14.6 | 0.85-0.98 | 0.92 |
| | A* | 1 | 9.2 | | 0.83 | |
| | B- | 13 | 7.4- 8.9 | 8.1 | 0.69-0.98 | 0.89 |
| | B* | 10 | 2.5- 3.7 | 3.1 | 0.58-0.67 | 0.63 |
| 5-58 | A- | 1 | 21.0 | | 1.25 | |
| | B | 11 | 9.1-16.9 | 13.2 | 0.84-1.18 | 1.04 |
| 6-58 | B | 10 | 30.9-32.1 | 31.5 | 1.67 | 1.67 |
| | B*- | 14 | 9.8-12.0 | 10.7 | 0.84-1.08 | 0.98 |
| | C | 7 | 16.2-19.5 | 17.8 | 1.34-1.68 | 1.50 |
| | C* | 8 | 3.8- 5.8 | 4.9 | 0.66-0.92 | 0.81 |
| 7-58 | B- | 4 | 13.7-14.5 | 14.0 | 1.46-1.51 | 1.48 |
| | C- | 13 | 10.2-14.4 | 12.1 | 1.35-1.53 | 1.41 |
| | C* | 10 | 3.1- 5.8 | 4.5 | 0.50-0.82 | 0.68 |
| 8-58 | C | 10 | 6.0- 7.2 | 6.7 | 1.10-1.18 | 1.15 |
| | C* | 9 | 0.4- 0.7 | 0.5 | 0.38-0.50 | 0.41 |
| 9-58 | C | 13 | 0.7- 1.5 | 1.1 | 0.35-0.66 | 0.44 |
| 10-58 | C | 11 | 11.5-15.1 | 13.2 | 1.25-1.43 | 1.34 |
| | C* | 9 | 4.1- 6.5 | 5.0 | 0.75-0.83 | 0.79 |
| 11-58 | C | 14 | 16.0-18.7 | 17.5 | 1.25-1.43 | 1.35 |
| | C- | 11 | 6.0- 7.0 | 6.5 | 0.78-0.92 | 0.85 |
| | A | 13 | 6.1- 7.8 | 7.0 | 1.23-1.33 | 1.28 |
| 12-58 | C | 9 | 17.0-19.4 | 18.1 | 1.48-1.60 | 1.53 |
| | A | 10 | 7.2- 8.4 | 7.8 | 1.26-1.34 | 1.30 |
| 1-59 | C* | 9 | 3.4- 3.8 | 3.6 | 0.80-0.85 | 0.83 |
| | A | 12 | 9.3-12.8 | 10.9 | 1.33-1.67 | 1.51 |
| 2-59 | A* | 11 | 1.2- 1.8 | 1.5 | 0.37-0.50 | 0.43 |
| | A | 10 | 28.0-29.3 | 28.6 | 1.75-2.00 | 1.85 |
| 3-59 | A* | 10 | 4.8- 6.7 | 5.6 | 0.65-0.83 | 0.74 |
| | A- | 12 | 7.6-11.5 | 9.5 | 0.87-1.14 | 0.96 |
| | B* | 10 | 2.0- 3.5 | 2.8 | 0.58-0.71 | 0.65 |
| 4-59 | A- | 8 | 12.8-16.6 | 14.2 | 0.84-0.99 | 0.91 |
| | B* | 11 | 2.1- 3.1 | 2.7 | 0.57-0.67 | 0.64 |
| | B- | 10 | 6.9- 9.8 | 8.5 | 0.75-0.96 | 0.87 |
| 5-59 | B | 13 | 8.5-16.3 | 12.8 | 0.87-1.20 | 1.05 |
| 6-59 | B | 12 | 25.1-30.8 | 27.4 | 1.63-1.68 | 1.65 |
| | B*- | 12 | 6.2-11.4 | 10.0 | 0.79-1.04 | 0.91 |
| | C | 4 | 16.4-20.0 | 18.1 | 1.40-1.61 | 1.51 |
| 7-59 | B- | 5 | 10.8-14.0 | 12.6 | 1.40-1.47 | 1.44 |
| | C | 10 | 21.3-28.1 | 23.2 | 1.51-1.73 | 1.63 |
| | C* | 12 | 3.0- 5.5 | 4.6 | 0.47-0.79 | 0.64 |
| 8-59 | C & C- | 8 | 6.7- 8.0 | 7.3 | 0.98-1.18 | 1.04 |
| | C* | 10 | 0.5- 2.0 | 1.2 | 0.43-0.58 | 0.51 |
| | B- | 5 | 8.0-10.1 | 9.0 | 1.20-1.31 | 1.24 |
| 9-59 | C | 12 | 0.7- 1.6 | 1.1 | 0.37-0.61 | 0.48 |
| 10-59 | C | 12 | 8.0-10.9 | 9.3 | 1.15-1.23 | 1.18 |
| | C* | 2 | 4.6- 5.0 | 4.8 | 0.68-0.74 | 0.71 |
| 11-59 | C | 12 | 12.8-15.8 | 13.8 | 1.20-1.38 | 1.28 |
| | A | 9 | 6.7- 8.0 | 7.2 | 1.16-1.31 | 1.23 |

* carrying eggs or young
- had carried young recently, signs of egg cases still on pleopods

three groups are plotted separately in Figure 2. However, in any one month the actual state of the ovaries of all non-ovigerous females is rather similar regardless of group, the heavier animals having heavier ovaries mainly because the ovary contains a larger number of eggs rather than eggs in a more advanced state of maturation. Table 3 which lists oocyte diameter and ovarian weight by group shows this clearly (see April, November). In most cases a single description in any one month will define ovarian condition in all non-ovigerous or in all ovigerous animals at that time. Figures 2 and 3 illustrate the sequence of ovarian changes.

January 1958. The ovaries of non-ovigerous females (Fig. 3, A) were large, the oocytes mature. The posterior lobe of the ovary was almost three times the length of each anterior lobe. The anterior lobes were rounded and thick. They curved backward dorsally over the heart and pressed against the carapace. The ovary extended from the bases of the first pereiopods to the bases of the second pleopods. The ovary of breeding females averaged 7.2 mg and was growing (Table 3).

February 1958. The ovaries of breeding

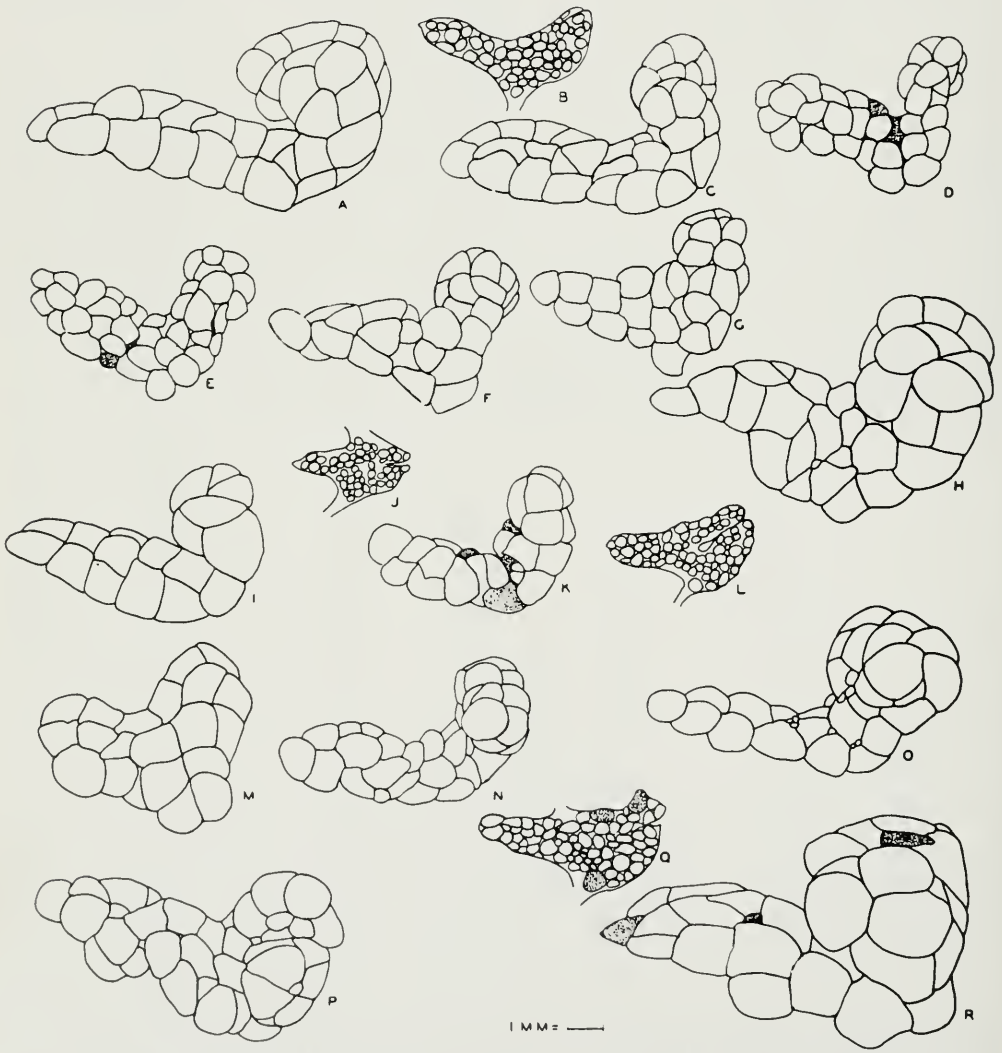


Figure 3. Annual cycle of ovarian development, January 1958 (3A) through February 1959 (3Q, R). See text for full explanation.

females were quite small and filled with new oocytes (Fig. 3, C). Those animals not carrying a brood retained egg cases; young had recently been present. The ovaries of this group had doubled their weight (Table 3) and retained the same general shape as present in January (Fig. 3, B).

March 1958. Group B had appeared and all were ovigerous. The animals of group A carried young or had molted after having a brood. About 5 percent of the oocytes present in recently molted animals showed yolk resorption, accounting for the decrease in ovarian weight. The posterior lobe of the ovary was more than twice the length of each anterior lobe (Fig. 3, D). The anterior lobes were elongated and narrow rather than rounded and thick as in January and February. The ovary extended from the second pereiopods just to the first abdominal segment.

April 1958. The animals carrying eggs had small ovaries, filled with new oocytes. The ovaries of the rest of the population had increased in size (Fig, 3, E) and were of the same shape as in March. Within an ovary the oocytes were not as uniform in size as previously; new oocytes were forming among more mature ones.

May 1958. Ovarian weight and oocyte diameter had increased (Fig. 3, F). The posterior lobe was approximately twice the length of each anterior lobe. Only 5 percent were brooding.

June 1958. In animals carrying broods the ovary (Fig. 3, G) was larger as contrasted with comparable groups in February, March and April, indicating a more rapid maturation of oocytes after egg-laying. In both ovigerous and non-ovigerous females the ovary was thick and compact, the posterior lobe only one and one-half times the length of each anterior lobe.

July 1958. Many of the non-ovigerous females still retained egg cases on their pleopods. The anterior lobes of the ovary were rounded and less than one-half the length of the posterior lobe (Fig. 3, I). The oocytes were larger than in June but had not increased in number.

August 1958. The ovaries of brooding animals were tiny, weighing only 0.5 mg and containing no oocytes larger than 0.42 mm (Fig. 3, J). This condition contrasts with that occurring in specimens collected in June when the ovary immediately began to increase in size and weight after egg-laying. The ovaries of those animals not carrying eggs or young averaged only 6.7 mg in weight and the oocytes were not uniform but of various sizes (Fig. 3, K). Yolk resorption was occurring; the ovary was reducing in size.

September 1958. No females carried eggs or young. The ovary was small, 1.1 mg, and extended from the bases of the third to the fifth pereiopods. The oocytes were round and of fairly uniform size; they were loosely arranged and one layer thick (Fig. 3, L), approximating the condition seen in immature animals.

October 1958. Fifteen per cent of the females carried eggs or young. The ovary of these animals weighed 5 mg and was growing. In those animals not carrying a brood the ovary averaged 13 mg in weight and oocytes measured 1.33 mm in diameter (Table 3). The ovary was thick and compact, extended from the second pereiopods to the end of the thorax. The three lobes were of about equal size. The anterior ones were upright with no backward curl (Fig. 3, M).

November 1958. Group A appeared in the population. The oocytes in this group underwent a slow maturation from November to February when there was a sudden increase in ovarian weight. In all females present in November the posterior lobe of the ovary was almost twice the length of the anterior lobes; the anterior lobes were beginning to enlarge laterally (Fig. 3, N).

December 1958. The ovary showed only a slight increase in weight over November. The posterior lobe had elongated to three times the length of the anterior ones. A few young oocytes were apparent (Fig. 3, O).

January 1959. Ten percent of the females were ovigerous. They represented the remnant of group C. The ovaries of the remaining 90 percent had the same general shape and extent as in December. While yolk deposition was occurring in the younger oocytes, resorption of yolk was beginning in some of the mature ones (Fig. 3, P).

February 1959. In brooding females the ovary was small and thin, but compactly arranged with little interstitial material (Fig. 3, Q). The largest oocytes measured 0.5 mm in diameter and represented old oocytes

from which yolk was being resorbed. Smaller, new oocytes were being proliferated. In those females which had not yet laid eggs the ovaries approximated the condition found in January 1958, but was heavier. Yolk resorption was occurring in about 10 percent of the oocytes (Fig. 3, R). This resorption was probably the result of forced retention of eggs past their maturation due to drought conditions at the end of 1958.

*Cement gland development.* — Cement gland development parallels oocyte maturation. The glands are not apparent in immature individuals. As the ovary approaches breeding condition the cement glands approach their fullest development. They decrease in size when egg-laying occurs and their secretion presumably provides the means of attaching eggs to the pleopods. After egg-laying the glands again begin to fill with secretion. Just as the ovary shows regression in late summer, so too do the cement glands, reducing to a stage of approximately 0.5, 0.0 in September from stage 4.0, 3.5 in July (Table 4). The sequence tabulated for 1958 also occurred during 1959.

The presence or absence of an externally viewed plug in the oviducts is also recorded in Table 4. The significance of this plug is not known. It appears to be composed of an amorphous or granular white secretion, probably from the ovary itself. It is not present in immature animals or in mature animals in September, but is present to some extent throughout the rest of the year, becoming very prominent and causing the thin exoskeleton covering the oviduct openings to bulge outward prior to egg-laying. Even when not apparent externally this white material may be found in the upper part of the oviduct. It appears to move down the oviduct and before egg laying is present only in the lower part of the duct. The substance is particularly prominent in the upper part of the oviduct and even in the ovary itself, near the duct, when yolk resorption is occurring.

*Discussion.* — The life span of female *C. shufeldti* is no longer than one year; that of an adult female, approximately six months, during which time she may produce two broods. Those animals which hatch in the late winter-early spring breed-

TABLE 4.
*Average monthly state of cement gland development (fifty specimens were examined each month).*

| Month | Group A | Group B | Group C |
|---|---|---|---|
| January 1958 | 2.0, 0.0, slight*–<br>4.0, 3.0, yes | | |
| February 1958 | 3.5, 1.0, yes<br>2.0, 0.0, yes– | | |
| March 1958 | 3.5, 2.0, yes | 1.5, 0.0, slight– | |
| April 1958 | 4.0, 2.0, yes | 3.0, 2.0, yes<br>2.0, 0.0, yes– | |
| May 1958 | 4.0, 4.0, yes | 3.5, 2.0, yes<br>4.0, 4.0, yes | 4.0, 4.0, yes |
| June 1958 | | 3.0, 0.0, yes– | 3.5, 0.0, yes– |
| July 1958 | | 4.0, 4.0, yes | 3.0, 0.0, slight–<br>4.0, 3.5, slight |
| August 1958 | | | 0.5, 0.0, slight–<br>1.5, 0.0, slight |
| September 1958 | | | 0.0, 0.0, no |
| October 1958 | | | 3.0, 0.0, slight–<br>3.5, 2.0, yes |
| November 1958 | 2.5, 0.0, no | | 3.5, 3.0, yes |
| December 1958 | 3.0, 1.0, slight | | 4.0, 3.0, yes |
| January 1959 | 4.0, 3.0, yes | | 2.0, 0.0, slight– |
| February 1959 | 2.0, 0.0, slight–<br>4.0, 4.0, yes | | |

* The first number refers to stage of lateral cement glands, the second to stage of midventral glands, "slight" refers to condition of oviducal plug.

– carrying eggs or young

ing season (group C) may mature and become ovigerous at a small size in late June, July and August. In 1958 group C could be subdivided into two parts: (1) those animals hatched near the beginning of the breeding season, and (2) those hatched near the end of it. Due to drought conditions, the 1959 group C corresponded only to (2) of the 1958 group. The larger of the group C animals may have a second brood in October. A very few of the smaller group C animals may survive the uary. The June young (Group A) do not winter and produce a second brood in Janattain sufficient size to reproduce until the following January and February. They reproduce only once. The young produced in late July, August and October (group B) reach maturity and may produce young in March and reproduce again in June.

The peaks of reproductive activity thus produced are in fair agreement with those published by Penn (1950) for *C. shufeldti*. His data included animals collected throughout the state of Louisiana. As local conditions vary, the expected flattening of the curve occurs; the peaks he reports are not quite so high nor the dips so sharp.

This is the shortest life cycle reported for any crayfish; others studied have been those of larger animals that required a longer time to reach maturity and lived longer in an adult condition (Hobbs, 1942; Penn, 1943; Smith, 1953). In these studies length was the only basis for separating different age classes. In *C. shufeldti* at least, length alone is not sufficient, as two distinct age groups, clearly demarcated by weight, may have overlapping cephalothorax length measurements. Thus weight and length together must be used to define age groups accurately in this small shortlived species.

### *Influence of Environmental Factors*

*Light.*—To determine the effect of day-length on the reproductive cycle, five groups of crayfish were maintained under different photoperiods from June 10 through September 15, 1958. The animals were collected on June 1, 4, 6, and 9, and not separated as to collection date. Males and females were present in each group. The crayfish were contained in covered rectangular stainless steel tanks, 49 x 37 cm, kept side by side in an air-conditioned laboratory. Water was changed weekly; the animals were not fed during the course of the experiment. Illumination was provided in each tank by one frosted 10-watt bulb suspended 20 cm above the water surface. Intensity of illumination at the surface of the water was approximately 40-45 foot-candles. Duration of light was controlled by automatic time clocks set to provide respectively 0, 6, 12, 18, and 24 hours of illumination daily. Illumination began at 6 AM.

Beginning July 1 and every fifteen days until September 15 a random sample of animals was removed from each tank and preserved in Bouin's fixative for future examination. As both group B and group C individuals were present during the early part of the experiment, the animals were weighed and cephalothorax length measured to separate the groups. The ovaries were dissected out, weighed and largest oocyte diameters measured. The results are summarized by group in Tables 5 and 6. Stage of cement gland development is also recorded in these tables.

In group B animals, darkness caused an initial increase in ovarian size and this increment was maintained through August 15, the last date on which animals of this group were present in the population. Exposure to six-hour day-length also caused increase in ovarian size but this was followed by a decrease in weight. For 12-, 18-, and 24-hour day-lengths there was a decrease in ovarian weight. However, with 18 and 24 hours illumination daily this initial decrease was followed by a weight increase.

The same general sequence was shown by animals of group C (Fig. 4). At the first sampling on July 1 these animals had just molted to a mature size and there was an increase in ovarian size in 15 days under all lighting conditions (Fig. 4, B, H, N, T, Z). A change from the situation in group B was that animals receiving a 12-hour photoperiod showed as great an increase as caused by complete darkness. By August 1 the ovarian weight of the animals in darkness was stabilized, while that of those under six-hour illumination showed an additional increase, and the other groups a decrease. By the middle of August the animals receiving 18 to 24 hours of light daily (Fig. 4, V, BB) showed an increase in

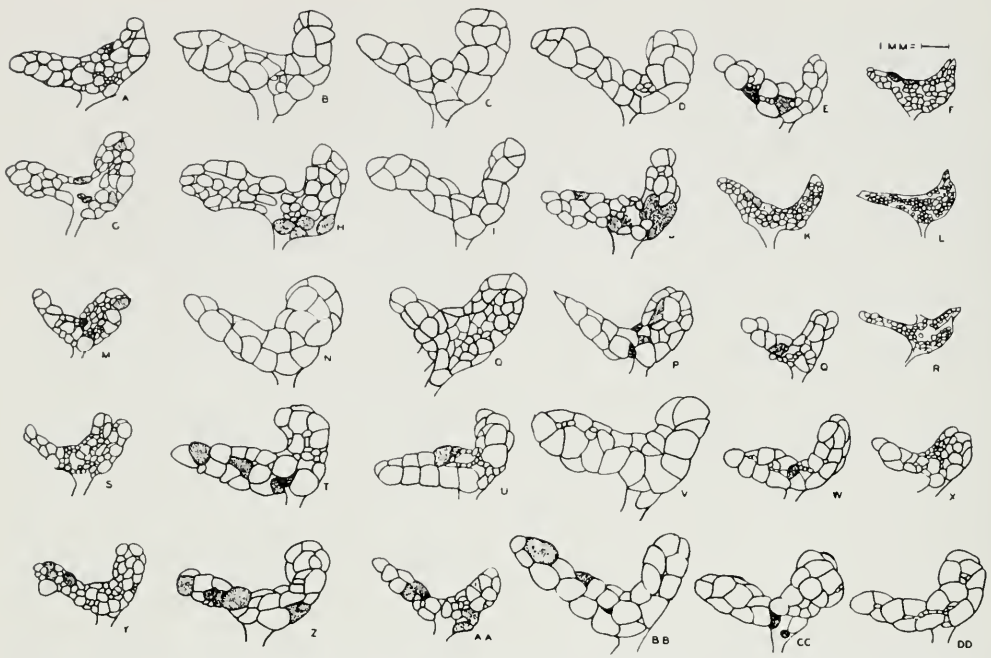

Figure 4. Changes in ovarian condition of group C crayfish in response to different photoperiods. 0 hours illumination, A-F; 6 hours, G-L; 12 hours, M-R; 18 hours, S-X; 24 hours, Y-DD.

ovarian weight while the others exhibited a decrease. In both September samples groups under all illuminations showed a decrease in ovarian weight, the most rapid decrease occurring in animals in darkness and the least rapid in those under continual illumination.

The cement glands generally followed the pattern shown by the ovaries (Tables 5 and 6). However, the correlation was not per-

TABLE 5.
*Changes in ovarian condition due to different photoperiods: group B animals.*

| Day-Length (Hrs.) | Date | Ovarian weight range | Ovarian weight mean | Oocyte diameter range | Oocyte diameter mean | Cement gland stage | No. of animals |
|---|---|---|---|---|---|---|---|
| 0 | 7-1 | 11.5-13.9 | 12.5 | 1.50-1.75 | 1.68 | 2.5, 0.0, slight | 9 |
| | 7-15 | 13.1-15.6 | 14.0 | 1.50-1.81 | 1.70 | 2.5, 0.0, yes | 8 |
| | 8-1 | 13.0-14.9 | 13.8 | 1.50-1.70 | 1.60 | 3.5, 1.5, yes | 5 |
| | 8-15 | 13.2-14.7 | 13.9 | 1.48-1.55 | 1.51 | 3.0, 1.0, yes | 5 |
| 6 | 7-1 | 10.5-12.5 | 11.7 | 1.52-1.67 | 1.60 | 2.5, 0.0, yes | 8 |
| | 7-15 | 10.9-13.0 | 12.2 | 1.50-1.73 | 1.60 | 3.0, 2.0, yes | 6 |
| | 8-1 | 7.7- 8.2 | 8.0 | 1.28-1.36 | 1.32 | 2.0, 0.0, yes | 4 |
| 12 | 7-1 | 10.5-11.9 | 11.2 | 1.51-1.70 | 1.62 | 2.5, 0.0, yes | 7 |
| | 7-15 | 9.7-10.8 | 10.3 | 1.41-1.54 | 1.47 | 2.5, 0.0, yes | 8 |
| | 8-1 | 7.9- 9.8 | 8.1 | 1.15-1.26 | 1.20 | 3.0, 1.0, yes | 6 |
| 18 | 7-1 | 10.2-12.0 | 11.1 | 1.56-1.65 | 1.60 | 2.5, 0.0, yes | 9 |
| | 7-15 | 9.1-10.9 | 9.7 | 1.20-1.47 | 1.38 | 3.5, 2.0, yes | 7 |
| | 8-1 | 9.2-11.1 | 10.5 | 1.40-1.49 | 1.44 | 3.5, 2.0, yes | 8 |
| | 8-15 | 14.4-16.9 | 15.9 | 1.44-1.62 | 1.55 | 4.0, 1.0, slight | 5 |
| 24 | 7-1 | 9.2-10.8 | 10.1 | 1.50-1.59 | 1.55 | 2.5, 0.0, slight | 5 |
| | 7-15 | 6.9- 7.9 | 7.6 | 1.19-1.25 | 1.22 | 2.5, 0.0, yes | 6 |
| | 8-1 | 8.5-10.7 | 9.5 | 1.30-1.39 | 1.35 | 3.0, 1.0, yes | 7 |

TABLE 6.
*Changes in ovarian condition due to different photoperiods: group C animals.*

| Day-Length (Hrs.) | Date | Ovarian weight range | Ovarian weight mean | Oocyte diameter range | Oocyte diameter mean | Cement gland stage | No. of animals |
|---|---|---|---|---|---|---|---|
| 0 | 7-1 | 2-1-3.8 | 3.2 | 0.85-0.91 | 0.91 | 2.5, 0.0, slight | 6 |
| | 7-15 | 6.6-7.8 | 7.2 | 1.13-1.40 | 1.30 | 2.5, 0.0, yes | 7 |
| | 8-1 | 6.0-7.9 | 6.9 | 1.26-1.40 | 1.33 | 3.5, 2.0, yes | 8 |
| | 8-15 | 6.0-7.8 | 6.7 | 1.26-1.43 | 1.34 | 3.0, 2.0, yes | 6 |
| | | 1.9-2.1 | 2.0* | 0.65-0.69 | 0.67 | | 2 |
| | 9-1 | 1.4-3.0 | 2.1 | 0.63-0.91 | 0.78 | 1.0, 0.0, no | 10 |
| | 9-15 | 0.7-1.2 | 0.9 | 0.35-0.43 | 0.38 | 0.0, 0.0, no | 10 |
| 6 | 7-1 | 2.0-3.4 | 2.8 | 0.71-0.93 | 0.80 | 2.5, 0.0, slight | 7 |
| | 7-15 | 4.6-6.0 | 5.3 | 0.92-1.12 | 1.00 | 2.0, 0.0, yes | 9 |
| | 8-1 | 6.4-7.8 | 7.1 | 1.21-1.42 | 1.31 | 3.0, 2.0, yes | 8 |
| | 8-15 | 3.9-5.7 | 4.9 | 0.67-0.91 | 0.81 | 1.5, 0.0, slight | 7 |
| | 9-1 | 1.0-2.2 | 1.6 | 0.35-0.53 | 0.43 | 0.5, 0.0, no | 6 |
| | 9-15 | 0.5-1.0 | 0.8 | 0.25-0.33 | 0.30 | 0.0, 0.0, no | 5 |
| 12 | 7-1 | 2.0-3.0 | 2.4 | 0.60-0.71 | 0.66 | 2.0, 0.0, slight | 8 |
| | 7-15 | 6.0-8.4 | 7.4 | 1.31-1.56 | 1.40 | 3.5, 3.0, yes | 7 |
| | 8-1 | 5.0-6.1 | 5.6 | 0.89-1.06 | 0.97 | 3.5, 3.0, yes | 8 |
| | 8-15 | 2.8-3.5 | 3.2 | 0.81-0.97 | 0.89 | 3.5, 2.0, no | 9 |
| | 9-1 | 1.5-2.3 | 1.9 | 0.68-0.76 | 0.73 | 0.5, 0.0, no | 6 |
| | 9-15 | 0.3-0.9 | 0.5 | 0.21-0.30 | 0.25 | 0.0, 0.0, no | 10 |
| 18 | 7-1 | 1.9-3.3 | 2.4 | 0.42-0.75 | 0.60 | 2.5, 0.0, slight | 6 |
| | 7-15 | 5.2-6.4 | 5.9 | 0.98-1.08 | 1.04 | 3.5, 1.0, slight | 7 |
| | 8-1 | 3.4-4.5 | 3.7 | 0.87-0.98 | 0.93 | 3.0, 0.0, no | 7 |
| | 8-15 | 6.5-8.0 | 7.4 | 1.32-1.47 | 1.40 | 4.0, 4.0, yes | 6 |
| | 9-1 | 2.5-4.2 | 3.2 | 0.78-0.91 | 0.85 | 3.0, 1.0, slight | 8 |
| | 9-15 | 1.0-3.0 | 1.7 | 0.69-0.75 | 0.72 | 3.0, 1.5, slight | 11 |
| 24 | 7-1 | 1.5-3.0 | 2.1 | 0.69-0.76 | 0.73 | 2.5, 0.0, slight | 9 |
| | 7-15 | 3.9-5.4 | 4.5 | 0.85-0.95 | 0.90 | 3.0, 0.0, yes | 8 |
| | 8-1 | 2.5-3.9 | 3.2 | 0.99-1.10 | 1.06 | 2.0, 0.0, yes | 8 |
| | 8-15 | 6.3-7.7 | 7.0 | 1.41-1.53 | 1.47 | 4.0, 4.0, yes | 8 |
| | | 2.0-2.4 | 2.2* | 0.85 - | 0.85 | | 2 |
| | 9-1 | 3.2-5.0 | 4.1 | 1.06-1.17 | 1.12 | 3.0, 2.0, yes | 9 |
| | 9-15 | 1.1-3.0 | 2.0 | 0.72-0.84 | 0.78 | 3.0, 2.0, slight | 10 |

* ovigerous

fect. In darkness there was a time lag in the maximum gland development and then the glands decreased while the ovarian weight remained steady. In group B animals from July 1 to July 15 there was no decrease in cement gland stage although three of the groups showed decreased ovarian weight and oocyte diameter.

The longer the photoperiod, the greater the cement gland development; only under 18- and 24-hour day-lengths did the glands reach the fully mature 4.0, 4.0 condition. For approximately the same ovarian weight the glands of animals exposed to long day-lengths were more fully developed.

The only animals to lay eggs during the course of the experiment were animals maintained in constant darkness and in continual light. Two animals of each of these groups were ovigerous on August 15 (Table 5). While this fact is interesting the samples were not large enough to determine the significance of egg-laying by members of these two groups.

Duration of light also had an effect on the ovaries of immature animals of 7.0, 7.5, and 8.0 mm cephalothorax length (Table 7). These animals were present only in three tanks; 0, 12, and 18 hours light. Although these data are meager, the average representing never more than five animals, the greater ovarian maturation of those exposed to 18 hours illumination was very marked. There was a steady increase in ovarian maturity as exposure to long day-length continued and by September the

TABLE 7.
*Average ovarian weights of immature animals exposed to 0, 12, and 18 hours light daily from June 10 to September 15, 1958.*

| Date | 0 hours Ovarian weight | 0 hours Oocyte diameter | 12 hours Ovarian weight | 12 hours Oocyte diameter | 18 hours Ovarian weight | 18 hours Oocyte diameter |
|---|---|---|---|---|---|---|
| 7-1 | .5 | .20 | .5 | .20 | .5 | .20 |
| 7-15 | .4 | .25** | .7 | .25* | .6 | .30 |
| 8-1 | .5 | .25 | .5 | .20** | .9 | .43* |
| 8-15 | .5 | .21* | .4 | .19 | 1.2 | .69 |
| 9-1 | .4 | .20** | .3 | .13 | 2.0 | .95 |
| 9-15 | .4 | .20 | .3 | .14** | 2.4 | 1.06 |

* two animals only ** three animals only
(The other measurements represent four or five animals)

oocytes had a diameter similar to that found in larger animals containing ovaries of 3 to 6 mg. A few crayfish of 6 mm cephalothorax length were present in the tanks, but ovaries of animals this small were indifferent to light conditions. They remained tiny, transparent threads containing minute oocytes.

Cement gland development paralleled ovarian development. The glands of animals in darkness and under 12 hours illumination remained undeveloped. Those under 18 hours illumination developed gradually to stage 3.0 (lateral glands), 1.0 (midventral glands) at the termination of the experiment. This degree of development was closely comparable to the stage 3.0, 1.5 of adult animals under the same conditions. This is in contrast to the results of G. C. Stephens (1952) who reported no increase in cement gland development in juvenile *O. virilis* subjected to long photoperiods. As the ovaries also remained in a juvenile condition, the animals used by Stephens might be comparable to the 6 mm *C. shufeldti* which were too young to respond.

This effect of photoperiod may explain why the ovaries of animals measuring 8.5 mm cephalothorax length were found in a mature condition only in July and August; exposure to long day-length for a period of time may be necessary to bring them to maturity. However, natural day-length is not long enough to cause animals smaller than 8.5 mm to mature.

A similar series of photoperiod experiments were undertaken beginning September 30, 1959. At the beginning of the experiment all crayfish possessed undeveloped ovaries. The only crayfish to survive an unscheduled spraying with insecticide were nine of the animals in darkness. Four of these were sacrificed immediately. October 28, and the remainder on November 28. These results are included because the response of the crayfish to darkness differed from the response in the summer experiments. The ovaries did not develop (Table 8. The small weight increase in November was due to proliferation of new oocytes and not to maturation.

*Temperature.*—To determine the effect of

TABLE 8.
*Changes in ovarian condition due to darkness: placed in darkness September 30, 1959.*

| Date | Ovarian weight range | Ovarian weight mean | Oocyte diameter range | Oocyte diameter mean |
|---|---|---|---|---|
| Darkness | | | | |
| 10-28 | 0.9- 2.9 | 2.0 | 0.35-0.62 | 0.47 |
| 11-28 | 1.8- 5.3 | 3.4 | 0.33-0.65 | 0.48 |
| Control (from Table 3) | | | | |
| 9-15 | 0.7- 1.6 | 1.1 | 0.37-0.61 | 0.48 |
| 10-15 | 8.0-10.9 | 9.3 | 1.15-1.23 | 1.18 |
| 11-15 | 12.8-15.8 | 14.3 | 1.20-1.38 | 1.28 |

TABLE 9.
*Changes in ovarian condition due to different temperatures: placed at constant temperature November 5, 1958.*

| Date | Ovarian weight range | Ovarian weight mean | Oocyte diameter range | Oocyte diameter mean | Cement gland development |
|---|---|---|---|---|---|
| 5.5-7.5°C. | | | | | |
| 11-22 | 1.4-2.8 | 2.1 | 0.60-0.74 | 0.67 | 1.0, 0.0, no |
| 11-29 | 1.9-4.5 | 2.8 | 0.60-0.95 | 0.81 | 1.0, 1.0, no |
| 12-6 | 2.5-6.1 | 4.0 | 0.67-1.00 | 0.82 | 3.0, 2.0, yes |
| 12-20 | 6.3-8.5 | 7.4 | 1.06-1.28 | 1.20 | 3.0, 2.0, yes |
| 14.5-19.5°C. | | | | | |
| 11-22 | 4.0-5.5 | 4.8 | 0.78-0.95 | 0.87 | 2.0, 0.5, no |
| 11-29 | 4.5-7.5 | 6.0 | 0.87-1.13 | 1.00 | 2.5, 1.0, yes |
| 12-6 | 5.0-8.2 | 6.4 | 0.92-1.13 | 1.00 | 2.5, 2.0, yes |
| 12-20 | 6.5-9.5 | 7.6 | 1.23-1.33 | 1.27 | 3.0, 2.0, yes |
| 29.5-30.5°C. | | | | | |
| 11-22 | 4.6-6.7 | 5.6 | 1.24-1.30 | 1.27 | 2.5, 1.0, yes |
| 11-29 | 1.4-5.5 | 3.3 | 0.58-1.07 | 0.81 | 2.0, 0.5, slight |
| 12-6 | 0.8-2.1 | 1.5 | 0.43-0.83 | 0.65 | 1.0, 0.0, slight |
| 12-20 | 0.3-1.2 | 0.8 | 0.17-0.53 | 0.33 | 1.0, 0.0, no |

temperature on the reproductive cycle of *C. shufeldti*, groups of crayfish were maintained at 6.5°C, 17°C, and 30°C for a period of one and one-half months. The same type tank and lighting arrangement as used in the light experiments was employed. All groups received 12 hours light per day beginning at 6 AM. The 30°C temperature was maintained by a hot water bath equipped with thermostat, the 17°C by a refrigerator, and the 6.5°C by a constant temperature room. Variation in temperature was recorded by maximum-minimum thermometers. The mortality of the 6.5°C group was initially high and then decreased to a low level. Very few died in the other two groups. Both males and females of groups B and C were present in each tank but only group C females were dissected. The animals were not fed during the course of the experiment.

The ovaries were dissected in van Harreveld's saline solution, which is isotonic to the blood of fresh water crustaceans (van Harreveld, 1936). The ovaries were drawn in dorsal view. The wet weight of each ovary was recorded. However, as a constant amount of saline was not transferred with each ovary, they were later reweighed after preservation so these weights would be comparable to those of other experiments.

Table 9 summarizes the sequence of ovarian changes under the three different temperatures and Figure 5 pictures ovarian condition. The animals were placed at constant temperature on November 5 and sampled at frequent intervals. At 17 ± 2.5°C the ovarian development was similar to that of animals collected in the field. The ovaries from animals in the December 15, 1958, field collection averaged 7.8 mg and had an average oocyte diameter of 1.30 mm (Table 3) while the experimentals dissected December 20 averaged 7.6 mg with an oocyte diameter of 1.27 mm.

The cooler temperature of 6.5 ± 1°C initially slowed development. However, the rate of development gradually increased so that by the end of the experiment the inhibition due to cold had been overcome and the condition of these ovaries and that of the 17°C group was similar.

Placing animals at an elevated temperature, 30 ± 0.5°C, caused a rapid increment in the ovarian size followed by deterioration with resorption of already formed oocytes and only limited proliferation of new ones.

At reduced temperatures there was a continual proliferation of new oocytes (Fig. 5, A-D) scattered among the maturing ones. At 17°C this proliferation was not so apparent (Fig. 5, E-H) and at 30°C the development of new oocytes was greatly slowed, the ovary being filled largely with a transparent interstitial material (Fig. 5, I-L).

The series of experiments with temperature was repeated in February-April, 1959.

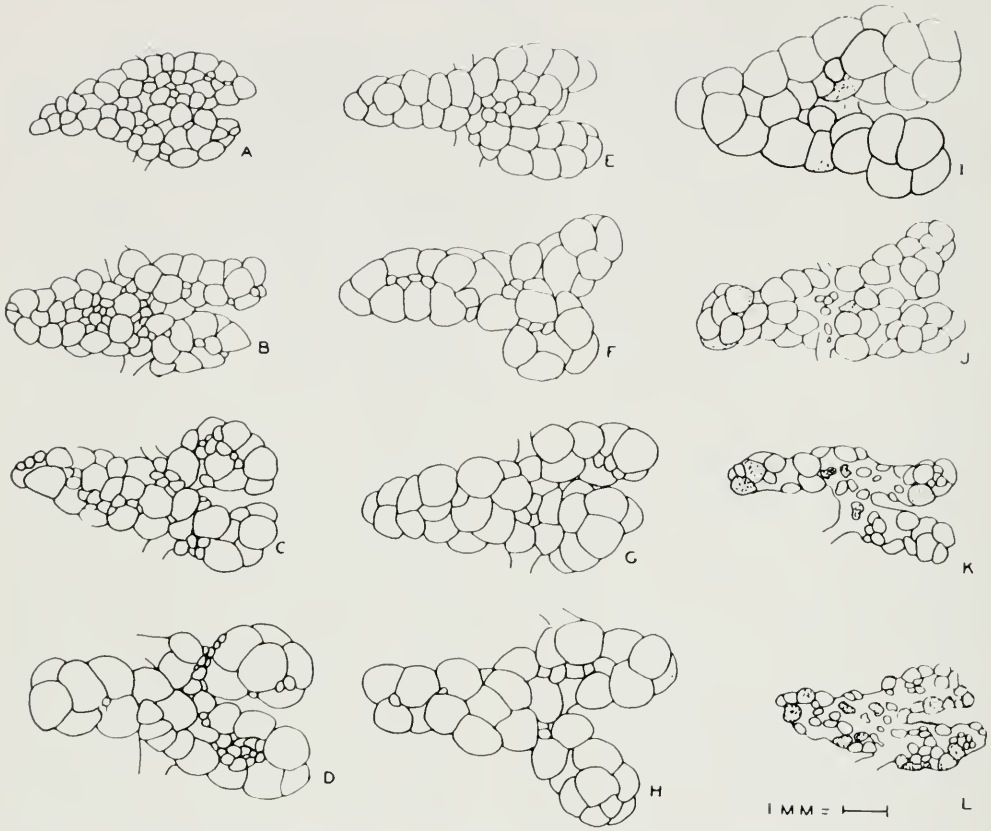


Figure 5. Sequence of changes in ovarian development under various temperatures. 7°C, A-D; 17°C, E-H; 30°C, I-L.

The low temperature was raised to 8.75 ± 1.25°C to lower the mortality that occurred at 6.5°. The high temperature was 28.75 ± 0.25°C rather than 30 ± 0.5°C. Only group A animals that were ovigerous at the start of the experiment were used. To minimize the possibility of the animals at higher temperatures resorbing the ovary as a food source because of their higher metabolic rate, strands of *Elodea* were placed in the tanks and some canned cat food added every other day.

Even with what was assumed to be an abundant food supply, the experimental results (Table 10) were essentially similar to those previously reported; a slowing of development at low temperatures and a sudden increase followed by resorption at high temperatures. However, the lag in ovarian development at low temperature increased with time rather than decreased. Also, the regression at a higher temperature proceeded at a slower rate and interstitial material did not replace the oocytes to as great an extent.

In the winter experiment cement gland development closely paralleled ovarian development, increasing or decreasing with ovarian development (Table 9). In the spring, however, cold temperature did not inhibit gland development; the glands of animals exposed to temperatures of 9°C were as fully developed as those of animals at 17°C (Table 10). The glands of animals at 29°C remained almost stationary at stage 3.0, 0.0.

Temperature affected the development of attached eggs and developing young. All animals carried eggs in which little development was apparent at the start of the 1959 experiment. At 29°C only two animals carried young at the time of the first sampling (18 days after the experiments began). The rest exhibited only empty egg cases because the young had already left the

TABLE 10.
*Changes in ovarian condition due to different temperatures: placed at constant temperature February 28, 1959.*

| Date | Ovarian weight range | Ovarian weight mean | Oocyte diameter range | Oocyte diameter mean | Cement gland stage |
|---|---|---|---|---|---|
| 28.5-29.0° C. | | | | | |
| 3-17 | 2.4- 2.9 | 2.7 | 0.55-0.74 | 0.65 | 3.5, 0.0, yes |
| 3-25 | 2.5- 4.9 | 3.9 | 0.67-0.80 | 0.73 | 4.0, 2.0, yes |
| 4-1 | 3.7- 5.6 | 4.8 | 0.87-0.97 | 0.93 | 4.0, 3.0, yes |
| 4-10 | 4.8- 5.6 | 5.2 | 0.87-0.98 | 0.94 | 4.0, 2.0, yes |
| 16-19° C. | | | | | |
| 3-17 | 1.7- 3.4 | 2.5 | 0.48-0.67 | 0.53 | 2.5, 0.0, slight |
| 3-25 | 4.1- 5.6 | 4.9 | 0.76-0.87 | 0.81 | 3.5, 1.0, yes |
| 4-1 | 6.5- 7.5 | 7.1 | 0.90-1.06 | 0.97 | 3.5, 1.0, yes |
| 4-10 | 11.9-13.7 | 12.8 | 1.06-1.23 | 1.12 | 4.0, 2.0, yes |
| 7.5-10.0° C. | | | | | |
| 3-17 | 3.8- 7.4 | 5.4 | 0.87-1.20 | 1.08 | 3.0, 0.0, yes |
| 3-25 | 3.0- 6.8 | 4.7 | 0.83-1.20 | 0.97 | 3.0, 0.0, yes |
| 4-1 | 3.0- 5.0 | 4.0 | 0.67-0.95 | 0.80 | 3.0, 0.0, yes |
| 4-10 | 2.8- 3.6 | 3.2 | 0.71-0.85 | 0.78 | 2.5, 0.0, slight |

pleopods. At 17°C, development was slower and a few young were still present on the pleopods after 22 days. A temperature of 9°C greatly slowed development; eggs were still present at the termination of the experiment, a total of 42 days. A few of these animals were then returned to room temperature and many of the eggs hatched in a few days.

*Discussion.* — Temperature, duration of

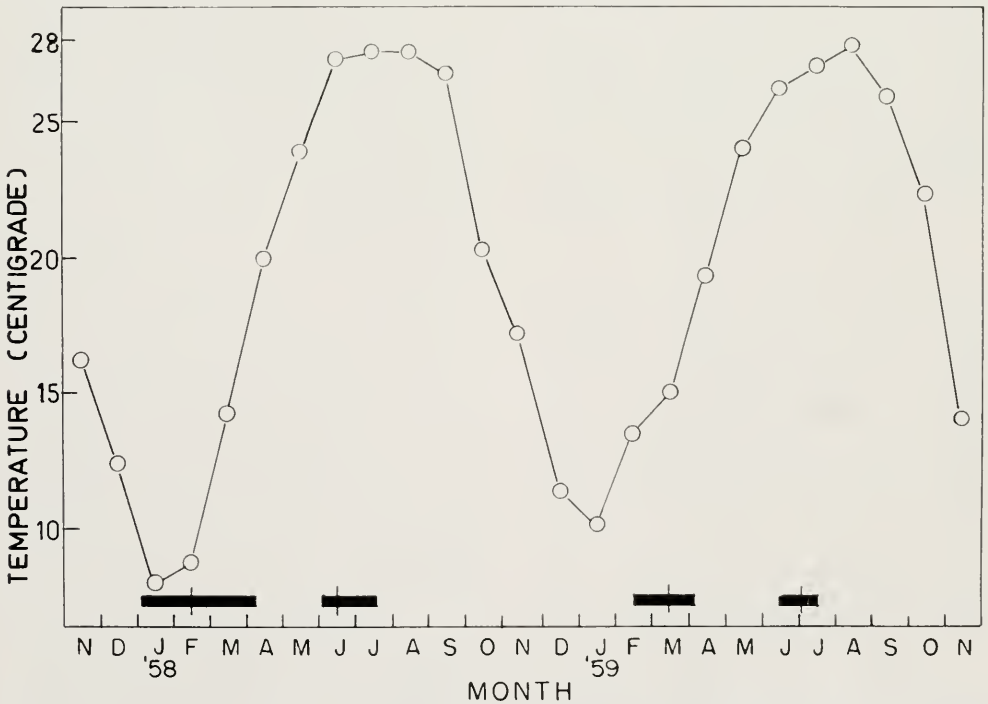


Figure 6. Annual variation in temperature at Slidell, La., expressed in terms of mean monthly temperature. The solid bars at the base of the figure indicate the period during which 60 percent or more of the females were brooding. The vertical line through each bar indicates the peak reproductive period.

light, and rainfall influence the reproductive cycle of *Cambarellus shufeldti.* The peaks of reproductive activity occur (1) in the coldest portion of the year, slightly after the shortest day-length, and (2) at the beginning of the hottest season which is also the time of longest day-length. Figure 6 shows the variation in mean monthly temperature throughout the year in the vicinity of the collection site. As the U. S. Weather Bureau does not maintain a temperature station at Pearl River, the temperatures recorded are from Slidell, Louisiana, eight miles southwest of the collection area. Figure 7 gives the variation in day-length throughout the year at New Orleans, Louisiana, 26 miles southwest of the collection site and at sea level rather than 29 feet elevation. The times during which 60 percent or more of the adult female population carried eggs or young are indicated by the horizontal bars on the figures.

The decreasing temperatures and shortening day-lengths of late fall and early winter stimulate proliferation of new oocytes and inhibit ovarian maturation. Short days tend to stabilize the oocytes as they develop rather than allow the quicker cycling of yolk deposition and resorption induced by long photoperiods. Gradually the inhibition induced by cold weather and short day length is lost, the ovaries mature and egg laying occurs.

As temperature is rapidly increasing toward the summer plateau, the young of the year grow and mature quickly. The ovaries of adult animals develop rapidly and there is a sharp peak of reproductive activity in June. Long day-lengths accelerate the cyclic activity of the ovary.

While the ovary in June and July grows very quickly after expelling eggs, continued high temperature induces yolk resorption and the ovaries regress until September, when they approximate the condition seen in immature animals. Day-length has been increasing from March through June and smaller animals are finally stimulated to mature and lay eggs in July and August before their ovaries also regress. The strong inherent tendency for the late summer decline is shown by the series of experiments with day-length.. The ovary regressed under all illuminations in September. That this may be associated with a general metabolic factor is shown by the fact that animals collected from the field in August and September exhibited less in body weight increase than in any other months during the year.

As cooler weather and shorter photoperiods set in, the ovaries begin to grow again, new oocytes are proliferated and a few animals are able to lay eggs before colder weather slows maturation of oocytes. The June young do not reach maturity before cold weather begins and are not able to reproduce until the following year.

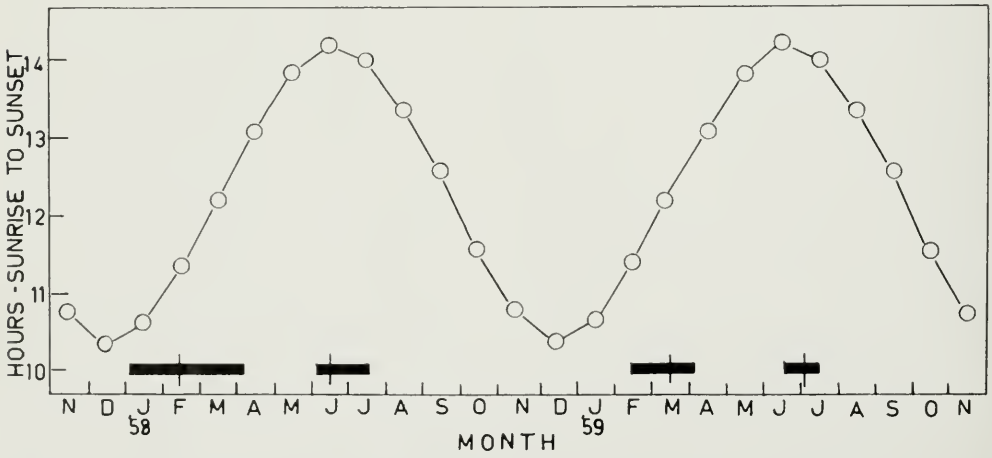


Figure 7. Annual variation in photoperiod at New Orleans, La., expressed as monthly mean number of hours from sunrise to sunset. The solid bars at the base of the figure indicate the period during which 60 percent or more of the females were brooding. The vertical line through each bar indicates the peak reproductive period.

Rainfall can influence the reproductive cycle to the extent that animals may be forced to burrow if rainfall is scanty. This occurred in December 1958 - January, 1959. The forced burrowing of the crayfish placed them in complete darkness and may give an extra spurt to ovarian development. The combination of cold and darkness, plus forced retention of the oocytes may account for the large size reached by the ovaries before the animals laid eggs in 1959.

Temperature has another effect on the reproductive cycle. Reproductive activity throughout the year was determined by the percentage of females carrying eggs or young. The time required for the eggs to hatch and for the young to leave the pleopods is inversely related to temperature. Mean monthly temperatures may vary from year to year and were lower during the 1958 winter breeding season than in 1959 so that, in effect, the period of peak reproductive activity was extended in 1958.

Lack of rainfall augmented the temperature effect in 1958-1959 by forcing the animals to burrow and thus delayed their breeding season. By the time standing water was again present, temperatures were warmer and the time required for the young to develop shorter; thus shortening further the span of the reproductive peak in 1959.

The data presented here agree with that of G. J. Stephens (1952) and Suko (1958). Stephen's experiments revealed that darkness stimulated maturation of oocytes and may inhibit cyclic activity, while increased light accelerated the cycle. Suko reported that oocytes of *Procambarus clarkii* kept in darkness for two to three months after oviposition displayed no histological change in spite of the elongation of their ovaries (indicating oocyte proliferation without maturation). Ovaries of animals kept further over this period developed earlier than those of controls. Animals kept in darkness immediately before breeding and egg-laying showed degenerative changes in the ovary.

*C. shufeldti* in the present experiments also showed varied response to lack of light depending on the time of year.

Further experiments on the effects of light are needed. Also in the present experiments, there was little difference between ovaries of animals exposed to 18 or 24 hours of light. The greatest day-length in New Orleans is 14 hours. How much the photoperiod can be reduced before distinct differences appear would be interesting to determine.

## Summary

1. The reproductive cycle of the female dwarf crayfish, *Cambarellus shufeldti,* is defined. While females carrying eggs on their pleopods can be found almost any time throughout the year, there are two peaks of reproductive activity, the largest in late winter-early spring, the other in June.

2. Three distinct groups of adult females appear in the population during the year. Individual crayfish probably live no longer than a year and no longer than six months as adults. During this time an animal may reproduce twice.

3. Increase of photoperiod induces a more rapid cycling of the maturation and resorption of oocytes. Decrease of day-length tends to stabilize the ovary in a mature condition at one time of year, while at another time tends to allow increased proliferation of oocytes without maturation.

4. Lowered temperature tends to slow maturation of oocytes while elevated temperatures cause a quick maturation followed by disintegration of the ovary.

5. *C. shufeldti* appears to have an inherent rhythm of reproductive activity, as shown by varied response to experimental lighting and temperature conditions at different times during the year.

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## Abstract

The reproductive cycle of the female crayfish *Cambarellus shufeldti* was defined. Field collections were made at least once a month from November 1957 through November 1959. While females carrying eggs on their pleopods could be found almost any time throughout the year, there were two peaks of reproductive activity, the largest in late winter-early spring, the second in June-July. These periods occurred shortly after the coldest portion of the year and shortest day-length and at the beginning of the hottest portion which is also the time of longest day-length.

Three distinct groups of adult females appeared in the population during the year as determined by total body weight and cephalothorax length. Individual crayfish probably lived no longer than a year and no longer than six months as adults. During this time an animal could reproduce twice.

Under increased photoperiod a more rapid cycling of maturation and resorption of oocytes occurred. Decreased day-length tended to stabilize the ovary in a mature condition or to allow increased proliferation of oocytes without maturation, depending on time of year.

Lowered temperature tended to slow maturation of oocytes while at elevated temperatures there was quick maturation followed by disintegration of the ovary.

# FECUNDITY AND REPRODUCTION IN THE LARGESCALE MENHADEN, *BREVOORTIA PATRONUS* GOODE[1]

ROYAL D. SUTTKUS
and
BANGALORE I. SUNDARARAJ,
*Department of Zoology, Tulane University, New Orleans, Louisiana*

## Introduction

There are no published accounts of observations on spawning of the largescale menhaden. Suttkus (1956) estimated that spawning occurred between October and February in the Louisiana area. The assumption was based on examination of a number of gonads during different seasons and by extrapolation and interpretation of length-frequency tabulations (Suttkus, 1956). In late fall schools of menhaden move to intermediate depths prior to spawning. This movement in the late fall is common knowledge to menhaden fishermen along the Louisiana coast. Moreover, waters off the mouth of the Mississippi River, where menhaden concentrate, are turbid most of the time, perhaps in part accounting for lack of observations on spawning.

## Materials and Methods

The 280 specimens used in this study were obtained between 1951 and 1958 along the east Louisiana coast. Most specimens were obtained by otter trawls.

### *Age Determinations*

Total length was measured from the anterior tip of snout to tip of the lower caudal fin lobe. Standard length was measured from tip of snout to posterior margin of hypural; the latter point was determined by flexing the caudal fin.

A scale sample was removed from the lateral area just above the tip of the appressed left pectoral fin of each fish. Each scale was read three times with the aid of a Bausch and Lomb microprojector.

### *Fecundity*

Most specimens were preserved in 10 percent formalin soon after capture and gonads were removed from specimens in the laboratory. Some gonads were removed from the specimens in the fresh condition, the volume was determined, and they were preserved in 10 percent formalin. These gonads were remeasured after preservation; thus volumetric statistics are consistent. The maximum volume of the gonads was reached in January (Figures 1 and 2).

Fecundity of the January specimens was determined by the volumetric method (Lagler, 1956) as follows: (1) the total volume in cubic centimeters of each ovary was determined after removal of excess moisture; (2) a small piece was removed from the middle portion of the ovary. The excess moisture was removed and the volume determined; (3) the number of large eggs in this piece was counted under a stereoscopic binocular microscope; and (4) the total number of large eggs in the entire ovary was determined by proportion. To estimate the extent of error in the above method, actual total counts of large eggs were made of ovaries of age groups I and II.

## Results

### *Age*

The scale method was used for determination of age after consideration of the findings of June and Roithmayr (1960). Table 1 shows a total-length frequency tabulation by age groups for two samples of menhaden which were collected on January 30 and 31, 1958. These specimens were obtained with a mid-water trawl from the Gulf of Mexico, latitude 29° 21′N, longitude 88° 55′W. We assume the two samples were part of a spawning group. The condition of the gonads (Figures 1, 2, and 3) is substantiating evidence. No age group IV individuals were present in the two January samples; however, 3 of the 280 specimens used in this study were of age group IV.

### *Fecundity*

Fecundity data determined by volumetric method and by actual count are presented in Table 2. The average percent error for two ovaries is 5.5.

[1] Partially supported by NIH RG-6279(RI), NSF G-3882 and NSF G-9026.

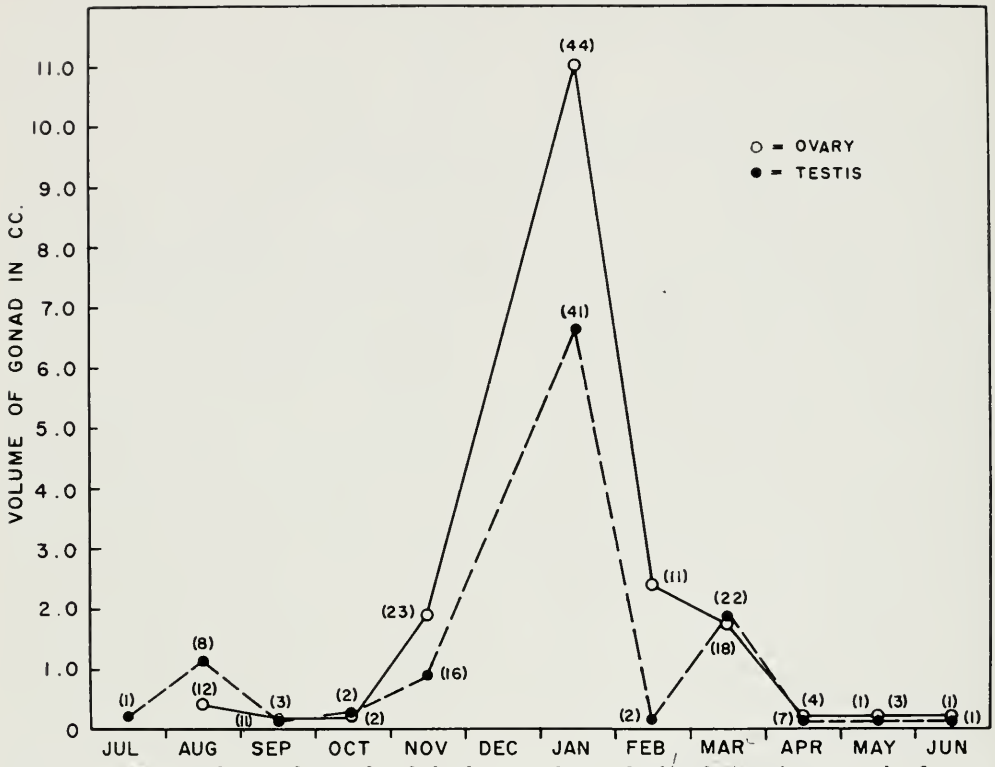


Figure 1. Mean volume of gonads of the largescale menhaden for various months for age groups I, II, and III. Figures in parentheses indicate number of specimens. (Based on collections of menhaden obtained in 1951 through 1958.)

The mean fecundity, total length, standard length, and volume of ovary, for various groups are shown in Table 3. The results show that fecundity increased with age and length.

*Reproduction*

Figures 1, 2, and 3 are based on composite samples obtained during the period 1951-58. There probably are slight fluctuations in the time of the spawning peak, from one year to the next as indicated by Suttkus (1956) on the basis of length-frequency tabulations. Moreover, the January peak shown in Figures 1, 2, and 3 is at the time of year during which spawning was estimated to occur. Apparently the enlargement of the gonads in preparation for spawning occurred during late fall, and spawning was finished during February and/or March. The illustrations in Figure 4 show the typical ovaries of age groups I, II and III (bottom to top respectively) during the months of August (left), January (middle), and March (right). The great reduction in volume of the spent ovaries is obvious by comparison of photos taken in January and March. The firm

TABLE 1.

*Total length distribution of age groups of two samples of largescale menhaden collected on January 30 and 31, 1958*

| Length interval in millimeters | Age group | | |
|---|---|---|---|
| | I | II | III |
| 170-174 | 1 | — | — |
| 175-179 | 2 | — | — |
| 180-184 | 2 | — | — |
| 185-189 | 1 | 1 | — |
| 190-194 | 1 | 8 | — |
| 195-199 | 1 | 12 | — |
| 200-204 | — | 21 | 1 |
| 205-209 | — | 15 | — |
| 210-214 | — | 13 | — |
| 215-219 | — | 3 | — |
| 220-224 | — | — | 2 |
| 225-229 | — | — | — |
| 230-234 | — | — | 1 |
| Number of fish | 8 | 73 | 4 |
| Percentage of total | 9.4 | 85.9 | 4.5 |
| Mean total length | 182.6 | 202.7 | 219.5 |

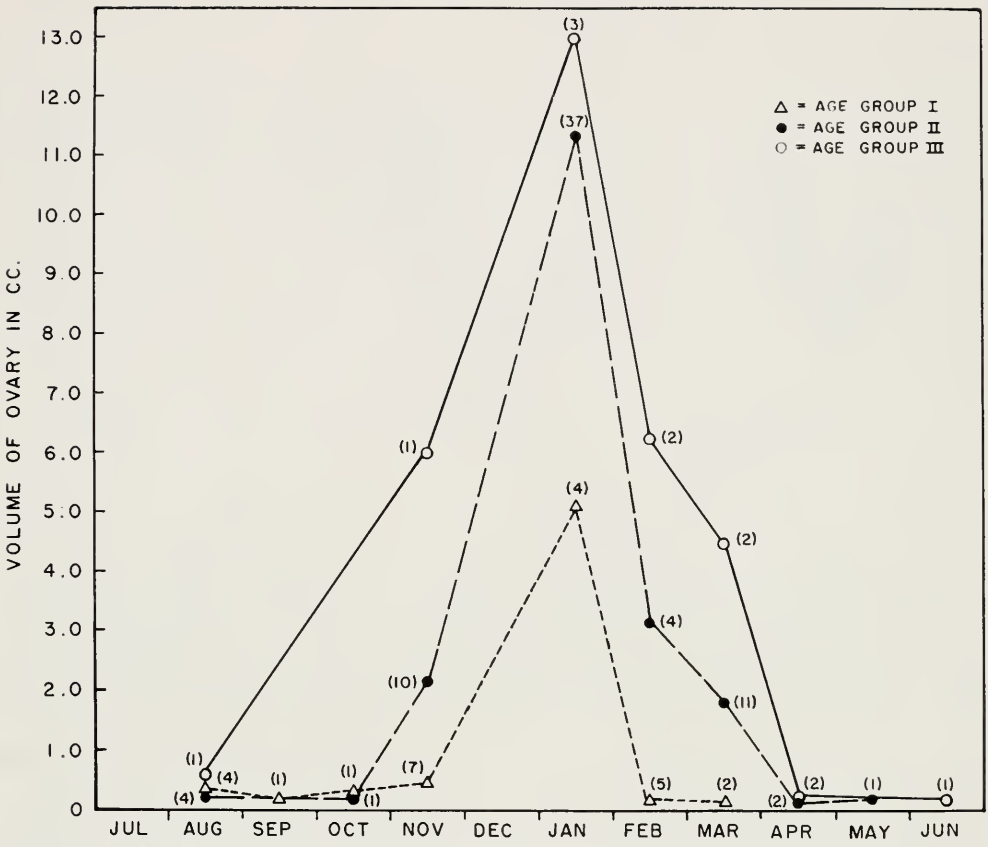


Figure 2. Mean volume of ovaries of largescale menhaden for various months for age groups I, II, and III. Figures in parentheses indicate the number of specimens. (Based on collections of menhaden obtained in 1951 through 1958.)

TABLE 2.

*Comparisons of estimated and actual fecundities in the largescale menhaden*

| Date collected | Age group | Total length in millimeters | Volume of gonad in cc. | Estimated number of eggs | Actual number of eggs | Percent error |
|---|---|---|---|---|---|---|
| January 31 1958 | I | 176 | 4.0 | 21,960 | 20,827 | —5.4 |
| January 30 1958 | II | 208 | 10.0 | 36,000 | 34,059 | —5.6 |

TABLE 3.

*Mean fecundity of 18 largescale menhaden collected in January, 1958*

| Age group | Number of specimens | Mean total length in millimeters | Mean volume of ovary in cc. | Mean number of eggs per female |
|---|---|---|---|---|
| I | 2 | 176 | 4.0 | 21,960 |
| II | 14 | 209 | 12.7 | 68,655 |
| III | 2 | 228 | 17.2 | 122,062 |

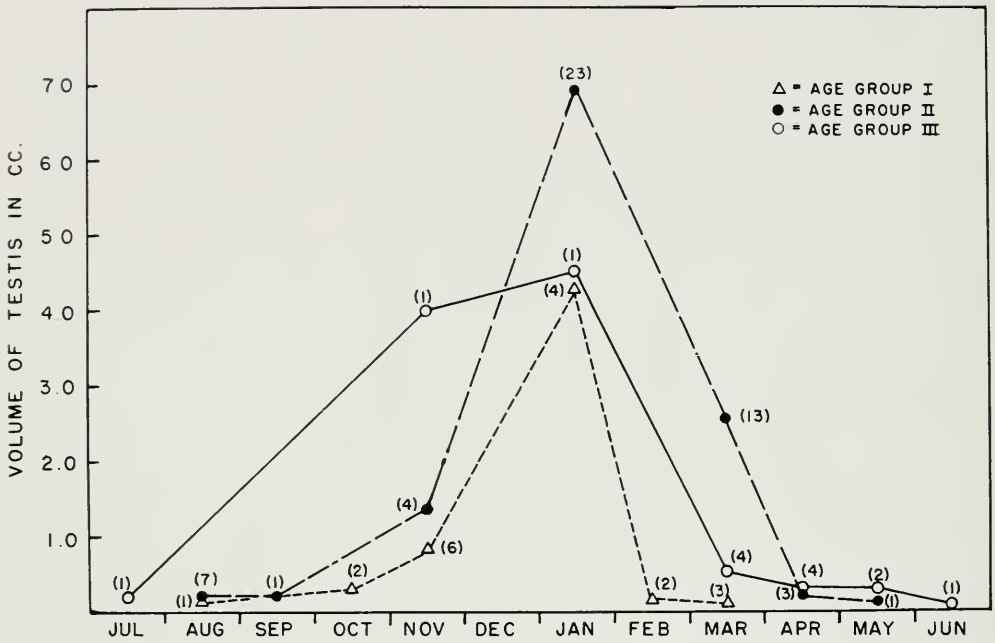


Figure 3. Mean volume of testes of the largescale menhaden for various months for age groups I, II, and III. Figures in parentheses indicate the number of specimens. (Based on collections of menhaden obtained in 1951 through 1958.)

texture and highly vascularized condition of the ovaries of those taken in January are also indicative of an ovary that is close to being spawned. The ovaries of the March samples were flaccid and the vascularization was degenerate. Age group II females of the January sample had an average gonad volume of slightly over 11 cubic centimeters whereas age group II males of the same sample averaged about 7 cubic centimeters. Part of the difference in volume is due to actual difference in volume of gonads of the same size individuals, though part is also due to the larger average size of the age group II females (Figure 5).

The January 30 and 31, 1958, combined sample was the only one that was of sufficient size to warrant analysis of age composition. In this sample age group II individuals made up 85 percent of the spawning population, age group I made up approximately 9 percent, and age group III about 4 percent (Table 1). Perhaps the most significant fact is that the largescale menhaden is a rapidly renewable resource.

## Acknowledgment

We gratefully acknowledge the aid given by the following persons: Stewart Springer and Harvey Bullis, United States Fish and Wildlife Service, for furnishing specimens taken by trawl off the mouth of the Mississippi River and to Robert Lee Eddy, Jr., formerly Chief of the Commercial Seafoods Division, Louisiana Wildlife and Fisheries Commission, for obtaining many of the samples.

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## Abstract

Fecundity of the largescale menhaden, *Brevoortia patronus*, from Louisiana coastal waters was estimated by volu-

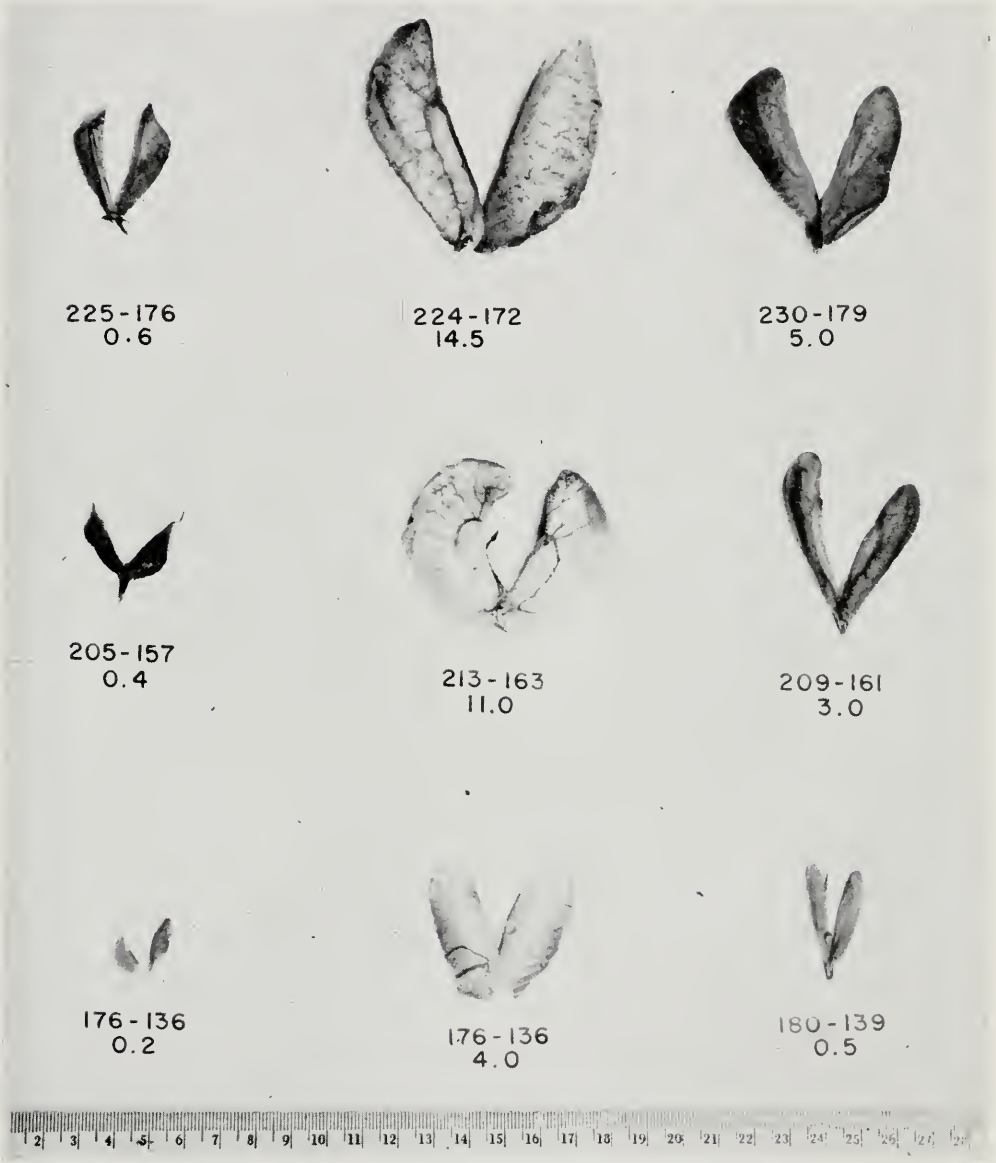


Figure 4. Ovaries of the largescale menhaden from age groups I, II, and III collected during August, January and March. Age group I (bottom row); age group II (middle row); and age group III (upper row). August sample (left column); January sample (middle column); and March sample (right column). The numbers separated by a hyphen are the total and standard lengths of the specimens and that below is the volume in cubic centimeters for the particular ovary illustrated.

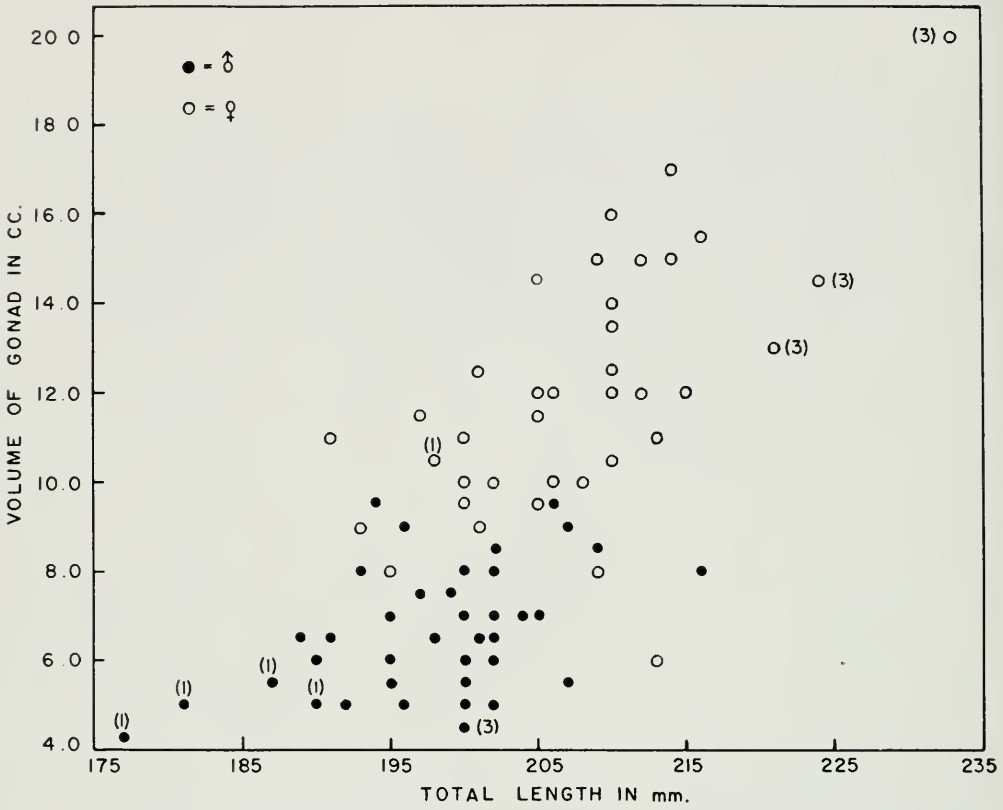


Figure 5. Relationship between total length and volume of gonad, based on part of two samples of the largescale menhaden collected on January 30 and 31, 1958. All menhaden except where otherwise noted on figure were age group II.

metric method. By actual count, we found 20,827 and 34,059 large eggs in the ovaries of one each of age groups I and II. Ovaries of age group II individuals averaged about four cubic centimeters more than the testes of the age group II males from the same spawning mass. Part of the difference in gonad volume was due to the larger average size of the age group II females. The period of the maximum volume of testes and ovaries in addition to texture indicate a spawning peak in January. Age group II individuals make up the major part (about 85 percent) of the spawning population, age group I about 9 percent, and age group III about 4 percent. The short life and early maturity make the largescale menhaden a rapidly renewable resource.

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